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Enhancing Biodiversity on Reclaimed Lands

by

Darlene Rose Howat

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Enhancing Biodiversity on Reclaimed Lands submitted by Darlene Rose Howat in partial fulfillment of the requirements for the degree of Master of Science in Land Reclamation and Remediation.

M. Anne Naeth
Dr. M. A. Naeth
Supervisor

M. J. Dudas
Dr. M. J. Dudas

Donald J Pluth
Dr. D. J. Pluth

R Currah
Dr. R. S. Currah

April 14, 1998
Date

ABSTRACT

The use of native species in land reclamation is important in conserving native habitat, but little is known about how native plant communities develop from a seed mix and whether saline soils will influence the formation of unique native plant communities. A plant community of native grasses and forbs was studied during the third and fourth growing seasons. The seed mixes of six to twelve species have a consistent diversity of three to four species and the significant variability in the density of seeded species has increased from year three to year four. The proportions of the seed mix were maintained in the plant community in 70 percent of the treatments. The most common seeded species were: *Agropyron trachycaulum*, *A. smithii*, *A. subsecundum*, *Bromus anomalus*, *Poa palustris* and *Achillea millefolium*. No consistent vegetation patterns coincided with soil electrical conductivity.

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Mae Elsinger

Pola Genoway

Suzanne Gill

Kirsten Gregorwich

Ted Harms

Robin Lagroix-McLean

Tamara Lamb

Emmanuel Mapfumo

Tanya Moskal

Kelly Ostermann

Wilf Petherbridge

Christine Pitchford

Jim Schaefer

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CHAPTER ONE
DIVERSITY, DENSITY AND COMMUNITY ASSEMBLY HYPOTHESES: AN INVESTIGATION OF PLANT-SOIL INTERRELATIONSHIPS

1.1 Introduction

Ecosystems are communities of organisms and their physical environment interacting as an ecological unit (Lincoln et al. 1982). Plant communities within an ecosystem interact through energy flows, element cycling and by modifying the microsites within the system. The diversity and density of plant species within an ecosystem varies temporally and spatially. Understanding the relationships between the structure of plant communities and how they function is a key goal of ecology (McCormick et al. 1974).

The interrelationships among plant species density and diversity and soil chemistry, particularly in salt-affected soils, are important in understanding how a plant community may evolve under specific conditions. For reclamation of disturbed lands, especially within native, undisturbed ecosystems, knowledge of how a plant community may evolve and what species will be present in the end point community is critical for restoration. Although the diversity and density of plant species is not only limited by soil chemical parameters, soil chemistry is an important domain to analyse since soil structure, nutrient availability and pH all interrelate to soil chemistry. Moreover, soil structure influences infiltration and other hydrologic characteristics of the soil, thereby affecting plant growth.

The topics presented in this chapter relate to plant growth and soil parameters and how they may influence plant density and diversity. Community assembly processes are discussed as an accompaniment to discern how the plant-soil interrelationships observed today may have evolved. Research techniques are important to the discussion of plant-soil interrelationships and community assembly processes in that some research methods may not lead to the provision of accurate information of current ecosystem processes. Within this chapter, a major emphasis has been placed on saline soils as they provide somewhat clearer delineations of soil-vegetation patterns relative to more subtle discriminations provided by other soils. Lastly, the relevancy of each density and diversity hypothesis for plant species on salt-

affected soils is analysed and the assembly processes of plant communities on salt-affected soils are discussed.

1.2 Species Diversity

1.2.1 Introduction

Diverse or "species rich" communities have minimum densities of 20 species m^{-2} (Grime 1973). In North America, the highest species rich community is in the savannas on the North Carolina coastal plain: 39 species m^{-2} on average, 52 species m^{-2} maximum (Shmida and Ellner 1984). The competitive abilities of plant species to obtain essential resources is thought to result in a competitive equilibrium in ecological theory. Species that are unable to obtain a limiting resource will be competitively excluded from an area, lowering diversity, but will not likely become extinct. Complete competitive exclusion is believed to be rare in nature (Hutchinson 1961; Miller 1967).

1.2.2 The Dynamic Equilibrium Hypothesis

There are numerous theories on plant community succession and Huston's (1979) research provides one theory. While Clement's (1916) theory includes stabilization as a "final cause" in the development of a climax plant community, the presence of a competitive equilibrium and competitive exclusion has been questioned by Huston (1979). With many factors in an environment changing constantly, a zero rate of change for all competitors, which must hold true for competitive equilibrium to be legitimate, is a rare occurrence. All plants are not in competition for all resources at the same time, as plant requirements for resources are likely staggered over the growing season. Instead, competition is centered around limiting resources, such as nitrogen, which are required simultaneously by many plant species and are changing in their abundance over time, including the species' lifetime. Alterations in the amount of a limiting resource can be perceived as changing the heterogeneity of the plant community. Genetic changes within a plant species may further alter the competition for resources if the requirement for a limiting resource is lessened in one species.

Huston (1979) believes the immediate outcome of competition within a plant community will be essentially the same, even if competitive equilibrium is not attained. Some species will increase in the community while other competitors will decrease,

regardless of the number of species within the community. The increased intensity of competition should theoretically decrease the species evenness and on an ecological time frame, the number of species will decrease. This is the inverse relationship between competition and species diversity. As low diversity results from intense competition, conversely low competition for limiting resources will produce a high species diversity.

1.2.3 The Dynamic Equilibrium Model

Huston (1979) speculates that by comparison of the rates at which various competitive abilities are expressed, diversity can be better understood. This approach may be more meaningful than simply comparing competitive abilities and can be viewed as the rate of competitive displacement. If a better competitor is located amongst a community of competing species that are increasing their competitive abilities at a slow rate, the better competitor will require more time to dominate the community. Therefore, if a community has a low rate of increase in its competitive abilities, less displacement of community members is anticipated. This enhances and maintains a greater diversity (species richness and evenness) over a much longer period than if the rate were higher.

Two interdependent factors maintain diversity and prevent a competitive equilibrium from occurring: a slow rate of competitive displacement and periodic population reductions (Huston 1979). As these two factors interact and a dynamic equilibrium is reached, plant community diversity may remain nearly constant over time. Over a sufficiently long time period, recurrent reductions of the population can be expected to occur, due to fire and insect outbreaks, for example. Similarly, the population growth rates of competitors within a community are generally constant as nutrients, light and temperature vary only slightly. If the frequency of population reduction is increased, its effect would be similar to a decline in population growth rates. When population growth rates and population reduction frequencies increase or decrease together, the dynamic equilibrium balance could essentially remain unchanged.

Species that may become extinct under conditions of competitive equilibrium may not become extinct during nonequilibrium conditions as the dynamic balance between the forces preventing equilibrium and the rate of competitive displacement

allow the coexistence of species to continue. For example, within a community having a rapid population growth of competitors, the dominant species would likely predominate sooner than if the population growth were lower for all species. Conditions that escalate population growth rates should have a lowered diversity while decreased growth rates should produce a greater species diversity. A longer period of coexistence is therefore possible when all species have decreased population growth rates.

Reduction of diversity could result if competitive exclusion or a high frequency of population reduction, without sufficient recovery times for all competitors, were to occur. Alternatively, for diversity to increase, the minimum time for all competitors to recover from a disturbance would have to increase as the frequency of reduction rises, leading to an increase in growth rates. As the ecosystem approaches competitive equilibrium, species diversity would decrease. If the frequency of reductions increases, the diversity of the community will actually decrease as some species will not have time to recover. Conversely, where population reduction is infrequent and competitor's growth rates are low, a competitive equilibrium will almost be attained and diversity will be low.

Overall, diversity should be greatest in communities where low to intermediate growth rates occur and population reductions are low to intermediate. Under these conditions, there is an opportunity for prolonged coexistence and provision of ample time for various compensatory components, such as fluctuating environmental conditions, to become effective. When change is gradual and not extreme, extinction is also less probable, therefore, diversity can remain high.

The dynamic equilibrium model also predicts what may occur in areas with an extremely unsuitable substrate or other extreme detrimental environmental conditions resulting in very low plant growth rates. Low plant growth rates may not be a predictor of high diversity in these situations, given the limited number of species that would be adapted to such a site. Since the model predicts that diversity will be high in areas of low growth rates, a threshold rate at very low growth rates may explain the relationship between plant growth rate and diversity. Below the threshold rate, diversity would remain low, while slightly above it, diversity would increase rapidly until a higher second threshold rate was reached, whereby diversity would decrease.

The dynamic equilibrium hypothesis (Huston 1979) and the several other theories that attempt to formulate plant community development are difficult to prove. Clement's (1916) theory is still debated by researchers today, which indicates that the complexity and variability present in plant communities provides a rich domain for further study and conversely a challenging area in which to construct definitive models and accepted theories.

1.2.4 Species Diversity and the Competition Index

The success of maintaining or reconstructing species rich plant communities is limited by competitive exclusion (Grime 1973). Plants considered to be competitive are characterized by: a) tall stature; b) a large, densely branched structure; c) relatively high maximum growth rate; and d) a tendency towards deposition of a thick litter layer. Plants can be scored according to each of these features and the sum of the scores provides a competitive index (CI) from 0 to 10 (Grime 1973).

When species diversity is high, vegetation with a high CI is found infrequently due to two mechanisms: environmental stress and physical damage. Environmental stress, can be induced by nutrient deficiencies and drought while physical damage and/or defoliation is caused by burning, trampling and/or grazing which prevents high CI species from reaching their maximum size and robustness and decreases litter drop. Therefore, species density is related to increasing environmental stress and physical damage and/or defoliation. When productivity is high and environmental stress is low, high CI species are able to attain maximum vigour and competitively exclude other species, resulting in low species density. When environmental stress is a factor, high CI species decline in vigour and species with low competitive ability are able to survive. As environmental stresses become more pronounced, productivity declines further, species diversity is reduced and limited to tolerant species. The decrease in productivity and species density is similar with increased intensity of grazing, mowing and trampling. This hypothesis is consistent with Odum's (1963) observations that the middle or moderate range of a physical gradient possesses the greatest diversity.

1.2.5 Environmental Heterogeneity Hypothesis

The premise of this hypothesis is that increased environmental heterogeneity will increase species diversity (Levin 1974). Spatial components of the environment generally operate to increase species diversity since the environment is heterogeneous. Initially, an area can be homogeneous, but through random events, such as colonization patterns, a series of interactions can be modified to create a heterogeneous environment. Environments that are initially heterogeneous become more heterogeneous through this process. Colonization of patches by founder species produces a variety of species mixes in unique proportions that will evolve differently from neighboring patches. Species with a limited ability to invade will be found in higher densities in their original microsites, with fewer individuals (lower densities) becoming established in new, less desirable, areas. Spatially continuous environments may evolve toward patchy ones by this process (Levin 1974) and patchy environments will tend to exhibit a greater species richness. The increase in species richness is due to patchiness in the environment and the existence of several types of patches will tend to reinforce the degree of species richness.

1.3 Species Density

1.3.1 Introduction

Abiotic (density-independent) factors limiting plant density to below the carrying capacity of the site are nutrients, water, light, climate, weather, space and safe sites for seed germination. Biotic factors that control density are predation, disease and stress in plant communities. These factors exert greater control over a plant community when density is high. After a disturbance, regeneration of a niche is highly dependent on the density of the surrounding or canopy vegetation as well as its composition (Shmida and Ellner 1984).

1.3.2 Density and the Dynamic Equilibrium Hypothesis

Huston's (1979) diversity hypothesis relates plant growth rates to density: low individual density is generally associated with low population growth rates. If one resource, such as a nutrient, is limiting to all individuals, growth rates and carrying capacity will be limited by this deficiency as well. Therefore, low density and low

growth rates will be the outcome. High growth rates are possible where there is a high turnover due to mortality, but typically low growth rates combined with a long time period and low mortality are the only way in which high densities are obtained.

1.3.3 Density and the Genetic Feedback Hypothesis

As one species becomes abundant and increases in density, competition for resources will become intraspecific rather than interspecific, due to natural selection (Shmida and Ellner 1984). Conversely, if a species is rare, or exists at a low density, interspecific competition is favoured and the rare species evolves into a superior competitor. This process has been documented in experiments with fly populations, but it is not known if it occurs naturally.

1.4 Density and Diversity Relationships

1.4.1 Diversity and Population Densities

Diversity may increase when population densities are low, as the mechanisms that allow coexistence are effectively increased (Huston 1979). "Low density may reduce the frequency of competitive interactions and change their nature as well" (Huston 1979). Competition for nonlimiting resources would be reduced when plant densities are low, so for example, competition for space between two species would not provide the plant with the competitive advantage in this area an opportunity to express that superiority. Both species could continue to coexist. Small temporal and spatial environmental differences may become unimportant at high densities, but may be sufficiently heterogeneous to segregate species at low densities. Huston (1979) provides an example using differences in soil parameters as a heterogeneous environmental factor. When plant densities are high, some individuals may overflow onto soils that are less preferred, thereby masking the differences in soil chemistry, texture or fertility. At lower densities, the differences in the soil may become more apparent as competition for space is minimized. Overall, low densities assist in maintaining the mechanisms for increasing or maintaining diversity.

1.4.2 Diversity and Disturbance

If a disturbance occurs, competition for resources is also likely to decrease as the damaged or removed individuals in the community reduce plant density (Shmida and Ellner 1984). With reduced competitive intensity, species from other diverse habitats may be able to move into the area and increase species diversity. However, biotic site modification by the dominant species may have occurred prior to the disturbance so that conspecifics would be favoured for regeneration rather than competitors.

1.4.3 Competitive Exclusion and Density

Koch (1974) found reductions in density can reduce the potential for competitive exclusion. The result of population reductions is to stabilize the community. For example, competitors who are superior in times of limited resource availability during the summer, when density-dependent growth produces competition, may have their populations reduced in the fall or winter by adverse conditions that reduce the populations of all species, but not necessarily by the same factor. The following spring, all species would have density-independent growth again and the cycle could continue indefinitely with coexistence maintained.

Coexistence may not be maintained, however, if there is an insufficient reduction in the populations so that density-independent growth does not occur the following spring. In addition, coexistence could be short-lived if two species, A and B, had the same growth rate. Species A must have a faster growth rate than B during the density-independent stage, while B must grow faster than A in the density-dependent stage, but coexistence may not be maintained even if this was to occur. If the growing season was reduced, coexistence of the species could not continue if growth was limited to the density-independent stage.

1.5 Interactions and Community Assembly Processes

1.5.1 Introduction

Communities are composed of spatially heterogeneous mosaic patches which are fragments of much larger ecosystems, and are known as metacommunities (Wilson 1992). Within communities, many complex interactions occur among species

which result in community patterns. These complex interactions are difficult to predict, may appear to be chaotic and can alter the dynamics of the ecosystem at the local and global scale. "One common feature of complex interactions, chaotic and otherwise, is sensitive dependence on initial conditions, in which small perturbations will have large effects on the outcome of deterministic interactions" (Wilson 1992).

Assembly processes relate to how plant species are formed into plant communities over time. The important influences on succession have been discussed among several researchers and there are many differing opinions on which assembly processes have scientific merit. Drake (1991) believes the history of the plant community accounts for the greatest distinction among plant communities and the reason why communities with similar species, trophic structures and other properties are different than expected. Conversely, Drake (1991) argues seemingly similar plant communities may have arisen from dissimilar origins but due to historical intervention may have developed to be currently highly idiosyncratic.

Competition for resources is commonly cited as a significant assembly process. Diamond's (1975) research indicates an ability to resist the invasion of a new species is one reason that adjacent plant communities with similar habitats often do not contain the same species. A second reason may be in the existing community's ability to use available resources optimally, thereby reinforcing the ability of the community to resist invasion (Diamond 1975). Tilman (1982) believes that competition among plant species "for inorganic nutrients influences community structure". Communities that become enriched with nutrients often have significantly lower diversity and the nutrient that is enriched becomes the overriding factor in determining which species achieves dominance (Tilman 1982). Additionally, Tilman (1982) believes the distribution of plant nutrients within a landscape closely correlates with the spatial and temporal distribution of plant species in a landscape.

A theory proposed by Pickett et al. (1987) incorporates all of the factors previously discussed as mechanisms of succession. Pickett et al. (1987) have developed a model of succession incorporating "all causes of succession in a complete mechanistic scheme". Using Clements' (1916) research as a basis for their model, it entails a variety of endpoints for a community to develop towards and does not have "a single or dominant mechanism or driving force" while being applicable to many ecosystems (Pickett et al. 1987). The model relies on the premise that the

availability of open sites is a prerequisite for succession to commence and that different species are available for moving onto that site. The species at a particular site have unique, evolved or enforced capabilities to deal with that site and the competition provided by the other species present. The "organism- and site-specific features are responsible for the great variety in the successions we observe" (Pickett et al. 1987). These specific features are quantifiable and provide a basis for predicting the pattern of species replacement. Some of the factors considered relevant are the size and severity of the disturbance, the seeds and propagules of plant species in the area of the disturbance, the resource requirements of the arriving species, the historical life differences among the species present in a community, competition and environmental stress (Pickett et al. 1987).

Community assembly processes are often synonymous with assembly rules and patterns. Assembly rules however, should be reserved for indicating the constraints or rules that govern the formation of the patterns and not the patterns themselves (Weiher and Keddy 1995). Many researchers indicate non-randomness or patterns are present, but they have not focused on the underlying processes or assembly rules which led to the formation of those patterns. Assembly rules are explicitly defined constraints that can be used to predict community structure (Weiher and Keddy 1995). These rules consequently influence the processes that occur to form plant communities. Grime (1979) developed a model based on competition, stress-tolerance and ruderals as the exclusive determinants of the member species of a plant community. The productivity of the habitat also influences succession and the corresponding plant biomass for each species (Grime 1979).

1.5.2 Variability in End Point Communities

End point communities can vary greatly, even if seemingly identical initially. In experiments, community ecologists discovered the replicates of treatments were as different in magnitude as the differences between the treatments (Hurlbert 1984). The subsequent interactions magnified these very small initial differences and provided evidence towards the sensitivity of the communities (Wilson 1992). Predation and competition are mechanisms that influence the end points of ecological communities and are thought to be well understood for some ecotypes (Drake 1991). However, inconsistencies result when using these processes to predict outcomes with similar

community types: patterns can vary between systems that have the same species composition and interspecific interactions.

1.5.2.1 Variability Due to Species Invasion Sequences

Communities with a shared regional species pool can be quite variable. The sequence of species invasion into individual communities may be the primary determinant of the community's uniqueness (Drake 1991). The variation of the sequence of species invasion would, in turn, modify the way in which the community was assembled and each community would become a representative of an alternative state. These states may be transient or persistent and are likely related to scale, which is a new area of research.

1.5.2.2 Variability Due to Historical Events

Past events within a community will influence the current state, so communities can be viewed as historically derived structures (Drake 1991). Alternative community states, when observed today may appear to be highly idiosyncratic compared to other local communities, but the trajectories that produced the alternative community states may reveal the differences are not that great. The mechanisms driving the variation may be indistinguishable from random events. The currently observed mechanics that are attributed with the formation of pattern may only be the mechanics that are responsible for maintenance of currently observed patterns. "The more fundamental organizational factors (e.g., the mechanisms ultimately responsible for community structure) may be hidden in the mechanics of community assembly" (Drake 1991).

Maintaining the pattern and causation of the pattern are likely often independent processes (Drake 1991). Many researchers have found the events that take place during community development, succession or the assembly process can generate differences in the community structure. These events or assembly processes are not visible in hindsight, but the events may have permanently influenced the structure of the community. The initial event may have created a situation that determines which other mechanisms are subsequently possible, especially if the community's species composition is altered. If different assembly trajectories can produce unique community states, it is uncertain whether only observation of extant ecological systems can disclose which mechanisms are responsible for production of

the observed pattern. To understand the mechanics of community assembly may assist in the development of a generalized theory of community level organization.

1.5.2.3 Trait Patterns

Consideration of species traits as an alternative to species names, may be more appropriate to finding patterns (Weiher and Keddy 1995). Coexisting species should display greater trait differences than expected by chance, using the principle of limiting similarity. If niche overlap is too large, then the coexistence of the two species is not possible. Community-wide patterns of limiting similarity have been called trait over-dispersion (Weiher and Keddy 1995). An example of this is the *Opuntia* cacti, that has no morphologically similar cogeners coexisting with it. This pattern of limiting similarity is common and has been researched for plants by Armbruster (1986), Cody (1991) and Armbruster et al. (1994).

Conversely, patterns where coexisting species exhibit more similar traits than expected by chance is known as underdispersion (Weiher and Keddy 1995). This trait has not been researched, although it significantly represents a restraint on membership in a plant community and a non-random pattern that may be observable within a community. Examples of trait similarity were found by Ratheke (1984) who observed the flowering phenology was more similar than would normally be expected by chance in one of two swamp sites. Within one community, Williams (1964) found more species per genus than chance would dictate. Therefore, if cogeners have greater similarity to each other compared to other species, then species that coexist should have fewer trait differences than expected by chance.

Using traits increases the value of assembly rules (Weiher and Keddy 1995). Assembly rules allow generalization between areas and habitat sites by utilizing information on traits, while species names do not. Secondly, focusing on traits "will help alleviate reliance on often murky taxonomy" (Weiher and Keddy 1995). Third, emphasizing traits will not be problematic if species are nearly interchangeable or identical. Fourth, use of traits will be more meaningful to a wider range of people, compared to species names. Lastly, rules based on traits will be simpler to read than a series of complex species interactions. An example of a trait-based rule is: "the proportion of species from each functional group will tend to remain constant for each observation" (Weiher and Keddy 1995).

1.6 Research Methods

1.6.1 Community Components versus Whole Communities

Analysis of communities to identify mechanisms and the resultant patterns is the main focus of community ecology. Typically, the research is confined to the study of some community components that is insufficient to reveal the connectivity of the community (Drake 1991). Ecological communities are ensembles of species delimited by the practical extent of species connectivity (Drake 1991). The connectivity of the energy flow, nutrient flows and other mechanisms by which the population dynamics can be influenced is important to understanding the processes within a community which cannot be studied by examining only the components of a community.

1.6.1.1 Historical Perspective

Since the assembly processes or events which may have permanently altered which other mechanisms are subsequently possible, are not currently visible, it is difficult to determine the magnitude of the differences between communities by observing their current patterns (Drake 1991). Therefore, as discussed in Section 1.5.2.2, it is important to determine the assembly rules and mechanisms that produced the patterns observable today.

1.6.1.2 Replication Accuracy

"Pseudoreplication is defined as the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated (though samples may be) or replicates are not statistically independent" (Hurlbert 1984). Replicates of an experiment encompass a degree of similarity that already exists or can be acquired among the experimental units. The importance of homogeneity in experimental work is generally well understood, but the use of replication of treatments is often overlooked. In designing an experiment, it is essential to consider the given or anticipated variability among the experimental units and to determine how many experimental units will be assigned to each treatment.

1.6.1.3 Use of Permanent Quadrats

In 1913, one of the first researchers to use permanent quadrats began studying meadow, fen and steppe vegetation (Markov 1985). Ramenskii, a Soviet scientist, recorded the proportion of species within permanent quadrats over a 10 year period and determined: "There is [sic] no stable groups of plants. The laws of formation of species groups but not the groups themselves are stable and these former [sic] must be investigated" (Ramenskii 1925). Although the species composition remained relatively consistent during the research period, the proportion of each species often changed significantly from year to year. Based on his results, Ramenskii (1925) believed plant communities are able to resist alien species invasion.

1.7 Soil and Vegetation Relationships

1.7.1 Introduction

Vegetative pattern formation can be produced by exposure gradients, temporal variation in environmental conditions, activities of herbivores, burrowing animals and insects, in addition to soil depth and nutrient availability (Moloney et al. 1992). Soil is one of the most important predictors of patterns, since it reflects the type of parent geologic material, passage of time, local climate, topographical position and type of vegetation that lead to its development. Soil and vegetation have an influential interrelationship that often results in vegetative patterns.

Plant species growth has been associated with specific microsites and soil quality parameters. Species and ecotypes are often classified in ecophysiological terms in accordance with their distribution in soils (Marschner 1986). For example, halophytes, acidophiles and metallophytes are associated with saline, acid and metallic soils, respectively. Many species have limited tolerance for some soil characteristics, such as minimum nutrient levels or high concentrations of aluminium, sodium and extreme values of pH.

Coexistence of many plant species "depends on the spatial patterning of suitable microsites, not just on the characteristics of the species and microsites" (Shmida and Ellner 1984). Researchers have observed vegetation patterns associated with changes in soil chemistry, soil depth and/or texture. For example, the

serpentine grasslands of Jasper Ridge exhibit a large scale pattern that sharply mirrors the distribution of the serpentine soils (Moloney et al. 1992).

1.7.2 Soil Chemistry

1.7.2.1 Macro and Micro Nutrients

The nutrients considered essential for plant growth can be divided into two categories based upon their relative abundance in plant tissues: macronutrients and micronutrients. Macronutrients are composed of nitrogen, phosphorus, potassium, sulphur, calcium and magnesium. The seven micronutrients essential for plant growth are: iron, zinc, manganese, copper, boron, chlorine and molybdenum. Additionally, some plant species also require these micronutrients: sodium, cobalt, vanadium, nickel and silicon. Micronutrients are as essential to plant growth as macronutrients, but required in much smaller quantities. If a nutrient in either category is available in excess or deficient quantities, it can prevent germination or reduce plant growth.

1.7.2.2 Cation Exchange Capacity

The availability of soil nutrients is directly affected by the cation exchange capacity (CEC) of the clay minerals and soil organic matter as the majority of soil nutrients absorbed by plants are cations. A negative charge on organic and mineral colloids attracts cations to the surface of the colloids and may neutralize the charge (Pritchett and Fisher 1987). The CEC is expressed as moles of charge per kilogram ($mol(+)kg^{-1}$) of oven dry soil. CEC will vary with pH as displacement of nonexchangeable hydrogen ions from structural -OH groups increase with pH. The -OH groups will attach to either organic matter particles or to the "broken edges" of clay minerals: both have a pH-dependent charge. With strongly acid soils, "these materials have neither a negative charge nor a cation-exchange capacity" (Hausenbuiller 1985). Permanent charges are associated with layer clays and are greatest for the 2:1 clays which include montmorillonite. In comparison, pH dependent charges are much smaller.

1.7.2.3 Acidic Soils

The pH of a soil is important to plant development as the availability of some nutrients is affected by pH. Soils with pH lower than 6.5 are generally considered to be acidic, due to the acidifying properties of organic matter, aluminium, carbon dioxide and presence of very low quantities of clay minerals (Tisdale et al. 1993). Changes in soil pH can be buffered by organic matter and clay minerals and therefore, coarse-textured soils or those with low organic matter do not have the same ability to maintain a constant pH and are usually acidic. The degree of acidification by soil organic matter or humus will vary with the type of vegetation, as coniferous vegetation has a lower pH than deciduous leaves.

Acidification is controlled by the carboxylic and phenolic reactive groups, within soil organic matter and humus, behaving as weak acids and dissociating, releasing hydrogen ions. Soluble salts are derived from organic matter decomposition, mineral weathering or manure. In acid soils, the cations of these salts will displace Al^{3+} and decrease the pH further. Aluminum is a common component of most soils with many multivalent forms and divalent metal cations will reduce soil pH more readily than monovalent metal cations.

The high concentration of H^+ ions is not the limiting factor to plant growth, but rather the toxicity of other nutrients at low pH values and/or the deficiency in essential nutrients that occurs as a result of acid soils limits plant growth (Marschner 1986). Acidic soils typically have higher levels of soluble aluminum and manganese, which at excessive concentrations, are both toxic to the majority of plant species. Reduced plant available nitrogen, phosphate, calcium and magnesium can be prevalent in acidic soils due to leaching. In some instances, low levels of sulphur, potassium, molybdenum, copper and zinc may also occur. Total and available nitrogen is very low in strongly acid soils and the available nitrogen is limited to NH_4^+ since nitrification is inhibited. Since many of the macro and micronutrients are found at low concentrations in acid soils, soil fertility is considered low.

1.7.2.4 Alkaline Soils

Alkaline soils have a pH greater than 7, due to the presence of $CaCO_3$ from a calcareous parent geological material. The $CaCO_3$ buffers the pH to 7.5 to 8.5 (Marschner 1986). When pH is greater than 8, soils are sodic or alkali and have a

sodium adsorption ratio (SAR) of 15 or more. Saline soils are commonly associated with sodic soils, but not all saline soils are alkaline and pure sodic soils are less abundant than saline-sodic soils. Salinity is considered a problem if it interferes with plant growth but the specific quantity of salt will vary with the plant species, water holding capacity of the soil, soil texture and salt composition. Therefore, the determination of whether a soil is saline is arbitrary. Generally in Alberta, $NaSO_4$ is the most abundant salt, but this will depend upon the solubility of the salts and the depth of the groundwater flows. The electrical conductivity (EC) and exchangeable sodium percentage (ESP) of a soil are typical measured with a saturation paste extract of the soil. If the EC is greater than 4 dS $m^{-1}$and the ESP is less than 15, the soil is considered saline, but the composition of the salts is not identified. The pH of saline soils is more variable, but it is usually near neutral with a tendency towards alkalinity. However, if a soil has an ESP greater than 15, it is classified as a saline-sodic or saline-alkali soil and will have high pH values.

Both calcareous and sodic soils have nutrient limitations (Marschner 1986). Calcareous soils have deficiencies in iron, zinc, phosphorus and occasionally manganese. In contrast, sodic soils are toxic in sodium and boron and deficient in zinc, iron, phosphorus and occasionally calcium, potassium and magnesium. However, nitrogen is the most limiting nutrient when soils are alkaline. Calcareous soils have different nutritional limitations than sodic soils due to their high concentrations of HCO_3^- and impeding soil physical factors, such as water deficits or root penetration ability. Sodic soils have the same problems as calcareous soils with the addition of poor aeration and generally poor physical conditions. Soil physical factors due to salinity and sodicity will be discussed in more detail in Section 1.7.3.3.

In low rainfall areas with alkaline soils, low soil moisture and water deficits in plants are constraints to growth (Marschner 1986). Phosphorus and potassium uptake by plants is dependent upon diffusion, so low soil moisture impairs the ability of the roots to obtain these nutrients. In alkaline soils, labile phosphorus may be limiting, so reduced soil moisture increases the severity of the problem. Zinc deficiencies are also related to low soil moisture and alkaline soils. In areas where moisture is not as limiting, lime-induced chlorosis can be detrimental to plant growth. This nutritional disorder occurs when $CaCO_3$ is greater than 20 percent and iron is deficient.

Anaerobic soil conditions tend to increase the likelihood of this problem, but the method by which high bicarbonate levels induce chlorosis is not fully understood.

1.7.3 Soil Physical Conditions

1.7.3.1 Soil Structure

The arrangement and grouping of soil particles is known as soil structure (Naeth et al. 1991). Alternatively, soil structure can be described as "the spatial heterogeneity of the different components or properties of soils" (Naeth et al. 1991). The components of soil structure are structural form, structural stability and structural resiliency. Structural form pertains to the solids and voids and their heterogeneous arrangement and is described by total porosity, pore size distribution and void continuity. The ability of a soil to maintain its structural form when stressed is the soil's structural stability. After a stress has been removed, the soil's ability to recover its original structural form through the natural processes of self mulching, mellowing and age hardening is known as structural resiliency.

1.7.3.2 Soil Nutrient Availability

Soil organic matter does not retain many nutrients, but is it still a critical component for soil fertility as it is the main source for some nutrients such as nitrogen. In some soils, 95 percent of the total nitrogen, 60 percent of the total phosphorus and 80 percent of the total sulfur may be contained in the organic matter. Since organic matter is concentrated near the soil surface, it is available to plants upon decomposition in proximity to the area of maximum root growth and nutrient absorption.

At pH 7.0, organic matter has the highest CEC of an exchange material at 100 to 300 $cmol(+)kg^{-1}$ (Hausenbuiller 1985). Montmorillonite clay has considerably less at 60 to 100 $cmol(+)kg^{-1}$. Generally, soils with a higher proportion of clay minerals are considered to have abundant plant available nutrients since the CEC of clay is high, relative to other soil minerals.

1.7.3.3 Soil Salinity

Salt and sodicity alter soil physical conditions. High concentrations of sodium combined with low concentrations of salts, cause soil aggregates to break down, reducing pore size, increasing bulk density and decreasing total porosity (Tisdale et al. 1993). When wet, dispersion of soil occurs due to the excess sodium ions which cannot bind the soil particles together into stable aggregates, causing puddling or slickspots. Sodium ions are hydrated and have a layer of water surrounding them that prevents tight adsorption to clay particles or aggregation between particles. When dry, a hard crust forms on the soil surface that can prevent germination and/or emergence of seedlings. Saline-sodic soils are highly aggregated. The salts compete for water with sodium and decrease the water layer around the sodium ion, causing flocculation.

1.7.4 Plant Growth and Soil Properties

Plant species tolerance for a particular environmental condition, such as xeric or saline conditions, does not imply the particular species has a physiological requirement for the conditions to survive and reproduce (Grubb 1985). However, tolerance for the extreme or unusual environmental condition is important as plants require the conditions they are normally associated with in their native environment to attain maximum growth rates. The adaptability of a species to a particular environment requires it have "key characters" that allow the plant to survive, in the presence of competitors, in that environment. To grow in a saline soil with a high salt concentration, a plant must have at least one of these key characters to ensure survival: "salt-sequestration in vacuoles, salt-exclusion at the roots or salt-secretion via glands or via evanescent, inflated leaf hairs" (Grubb 1985).

1.7.4.1 Plant Growth and Nutrient Availability

The dry weight of plants is 5 to 10 percent essential plant nutrients (Tisdale et al. 1993). Plant growth is a function of many factors and if one factor is limiting, increasing its quantity will generally increase plant growth. This is known as Liebig's Law of the Minimum and it is important for assessing plant nutrient limitations. Native species are often able to grow on sites that are considered nutrient deficient for agricultural crops. When phosphorus is limiting for crop species, deficiency symptoms can be observed, while native species adapted for this type of soil nutrient regime have

a relatively high phosphorus content and show no signs of deficiency. The contrast between the two plant groups is likely due to the marked difference in growth rates: native species tend to grow slower and are thereby able to use nutrients as they become available through mineralization.

Soil and plant root interactions can alter nutrient availability as root growth acquires nutrients from soil reserves and as roots increase the nutrient availability in two ways (Hausenbuiller 1985). Firstly, the creation of an acidic rhizosphere increases the solubility of the minerals where nutrients are found, so nutrients are released into the soil solution. Secondly, the uptake of nutrient ions by plants lowers the concentration in the soil solution, causing the release of nutrients from soil minerals to maintain the concentration levels.

The uptake of nutrients by one plant can affect the nutrient supply for other plants in the neighborhood and therefore, the growth of nearby plants (Huston and DeAngelis 1994). The most intense competition occurs over the resource that is most limiting to each plant species' growth. Nutrients with low mobility, such as phosphorus, or nutrients that are resupplied mainly through microbial activity, may not be sufficiently affected by the uptake of one individual plant to alter the availability to other plants. However, if a limited nutrient is transferred to a plant root by diffusion, the plant uptake lowers the concentration of the nutrient in solution within the immediate vicinity. In an area of many plants, survival of a specific plant depends on the local concentration of a nutrient around it to be equal to or larger than the smallest concentration it requires to survive. Either the supply of nutrient to the soil solution within a region must be at a high rate or diffused through the soil at a limited rate to "prevent a plant from strongly influencing the levels of nutrients available to its neighbors". If either of these factors are present, many competing species can coexist in a local area, even if the same resource is limiting to each of them.

1.7.4.2 Plant Growth and pH

Soil pH is an important factor in plant growth. Some plants that are native to calcareous soils (pH 7 to 8), are able to grow larger on soils with pH 5 to 6, but not all species exhibit this growth response (Grubb 1985). Two species with a equal tolerance "are not necessarily the most abundant in the same fraction of their tolerance

range" (Grubb 1985). One species may have a maximum tolerance for pH 4 to 6, while another may have maxima at pH 3 to 4.

In an experiment with *Plantago major* and *P. lanceolata*, the range of pH values in each species' habitat was analysed (Van Der Aart 1985). Within the 72 habitats where *P. lanceolata* was found, the soil pH varied from 4.3 to 7.8. *P. major* was discovered in 17 habitats where soil pH values were 5.3 to 8.4. Occupation of a wide range of pH values is evident for both species, indicating pH is not a limiting factor for growth in most cases. Plants of a different species may not have the same range of adaptability and may require a narrow range of pH values to survive (Grubb 1985).

1.7.4.3 Plant Growth and Soil Structure

Soil structure can have a significant impact on plant growth. The ability to obtain adequate water, air, nutrients and produce root growth are all affected by soil structure. The hydrologic properties of a soil can be negatively altered by poor aggregation, resulting in puddling after rainfall events or by compaction which reduces infiltration. Both soil conditions have a low volume of macropores and pore continuity which inhibits the flow of water and air throughout the soil solum and reduces root growth (Naeth et al. 1991). The mass flow or diffusion processes that carry nutrients to the plant roots are also disrupted when macroporosity is reduced. Adequate rates of oxygen diffusion through the soil is important to maintain sufficient partial pressure on the root surface (Tisdale et al. 1993). With agricultural crops, such as corn, increasing the rate of oxygen diffusion is more important to plant growth than having medium to highly fertile soils. Microbial activity and decomposition of organic matter is also impeded by poor soil aeration and inadequate water volumes, producing a slower release of nutrients. The strength of a soil can also interfere with root growth if water and nutrients are limiting (Naeth et al. 1991).

Structure is affected by plant roots. Lines of weakness produced by roots or root hairs entering into aggregates, may cause the aggregate to fracture into granule size fragments (Naeth et al. 1991). The materials secreted by roots can also alter soil structure within the immediate vicinity of the root. Aggregates can be cemented together, stabilized or soil particles flocculated. Dehydration and subsequently shrinkage and cementation occurs with plant water use, altering soil structure.

1.7.4.4 Plant Growth and Salt-Affected Soils

In addition to EC and ESP as indicators of soil salinity, another criterion can also be used: if soluble salts are present in sufficient quantities to affect plant growth, then the soil is considered saline (Marschner 1986). Plant growth is affected by high levels of sodium chloride and other salts and an impaired water balance. The high concentration of salts produces high osmotic pressure and potential toxicity to salt ions or chloride ions. Excluding the salt ions at the cell membrane will minimize toxicity but expedite water deficits while absorption of salt requires osmotic adjustment but can result in ion toxicity and nutrient imbalances (Marschner 1986). Assessment of the relative contribution of ion toxicity versus water deficit to the inhibition of growth is impossible when salt concentrations are high. In species that are not adapted to saline soils, low concentrations of salinity can cause growth inhibition due to ion toxicity.

During germination, the effect of salinity is at its greatest and results in bare patches of soil. Exposure to greater levels of salinity at the germination stage may be higher than at other growth stages (Hayward and Bernstein 1958). The surface layers of soil accumulate salts as evaporation and capillary rise occurs. Seed placement near the soil surface is within an area of salinity that is substantially greater than the average salt content in the top 10 to 20 cm of the soil surface. Moreover, the evaporation of moisture at the soil surface increases the osmotic pressure and moisture tension in that zone. The increased moisture tension amplifies the effect of the salinity at germination. It was discovered that "the first increments of salinity tend to retard germination and that additional increments tend to reduce progressively the final percent germination" (Hayward and Bernstein 1958). Moreover, the correlation of salt tolerance in germination to salt tolerance at later growth stages is poor.

The presence of sodium in the seed bed inhibits germination and emergence primarily by the dispersion of the soil, leading to poor aeration and surface crusting (Hayward and Bernstein 1958). If the soil physical condition can be made more favorable with a soil conditioner, an ESP of up to 60 percent will have little or no effect on the germination of beets (*Beta* spp.) or beans (*Phaseolus* spp.). Other plant species, such as clover (*Trifolium* spp.), were negatively affected by ESPs of 25 percent or less when a soil conditioner was used.

Native plant species were also tested for tolerance to salinity. Migahid and Ali (1955) "found the osmotic pressure of mesophytes, xerophytes and halophytes to be directly related to salinity and inversely related to the soil-moisture level" (Hayward and Bernstein 1958). The most decisive factor was soil salinity. Another researcher, cited by Hayward and Bernstein (1958), tested two halophytes (*Salicornia, Salsola*) and a number of crop species to determine a wilting coefficient. For most of the crop species, the wilting coefficient of the soils varied, depending on the plant species and additionally, the soil available moisture content decreased as the salinity increased. However, the wilting coefficient of the halophytes was constant or lowered with increased salinity.

1.8 Plant-Soil Microsites on Saline Soils and Transition Zones

Two studies were conducted on the Great Plains of the United States and one on the Northern Tablelands in New South Wales by separate researchers attempting to discern the vegetative patterns associated with salt-affected soils. Each researcher sampled soils and recorded the species composition and density where saline and/or sodic soils were known to exist, the transition zones and surrounding areas. Correlations between particular species and soil type were highly positive in some instances, especially in highly saline areas.

1.8.1 Plant-Soil Microsite Relationships in a Saltgrass Meadow

Soil characteristics and existing native vegetation were studied by McGinnies et al. (1976) to determine a possible relationship. A saltgrass meadow in Colorado was analysed for vegetative basal area in 47 permanent 1 m^2 quadrats within an area 4 km long and 0.2 to 0.6 km wide. Upon completion of the vegetative analysis, a soil sample was taken from the center of each quadrat. Soil samples were obtained by digging a pit to the depth of the C horizon (61 to 91 cm) and removing two slices of soil from each pit. In descending order, the dominant species found within the quadrats and their average actual basal area were: *Distichlis stricta* (saltgrass) 13.6 percent; *Sporobolus airoides* (alkali sacaton) 8.4 percent; *Bouteloua gracilis* (blue grama) 5.6 percent; *Carex filifolia* (threadleaf sedge) 3.6 percent; and *Agropyron smithii* (western wheatgrass) 2.3 percent. Average total cover for the 47 sample plots was 33.5 percent.

The relationships between vegetation and microsite were calculated (McGinnies et al. 1976). Saltgrass and Solonetzic soils were highly positively correlated as the delineation between saline soils and non-saline soils was mirrored by the saltgrass. The blue grama was very sensitive to salt: as salt concentrations decreased in the A and B horizons, the relative abundance of blue grama increased. The salinity of the C horizon could not be determined by blue grama since it has a shallow rooting depth. Thicker A horizons along with deeper C horizons supported plants with a greater basal area and height due to the higher water retention of the A horizon and a greater depth to the saline C horizon. Alkali sacaton was the most dominant species where these soils occurred, with 23.9 percent average basal area. Western wheatgrass was most abundant on clayey sites.

1.8.2 Soil and Vegetation Relationships in a Saltgrass Meadow

The relationships between soil types, salinity, sodicity, fertility and vegetative ground cover were studied by Bowman et al. (1985) in Colorado. Three transects were placed perpendicular to Eastman Creek and 48 soil samples (7.5 cm diameter cores, 60 cm deep) were taken along the transects and four 30 x 30 cm quadrats were placed at each core location to conduct vegetation sampling in June 1979, 1982 and 1983.

The soils in transects 1 and 3 had A horizons that averaged 30 cm in depth. Transect 2 soils had very shallow or absent A horizons in over half of the soil samples and had poor physical properties. The B horizons of transect 2 typically had a columnar structure and were impermeable to water. Overall, the values for SAR, pH and EC were highest along transect 2 at a depth of 0 to 20 cm. Within this soil zone, the following values were recorded: SAR 60+, pH 8.2 and EC 20.0 dS/m.

The vegetation reflected the soil conditions along each transect. Transects 1 and 3 had the greatest amounts of mixed vegetation and significantly less saltgrass than transect 2. Western wheatgrass was prominent only on transect 1 at 20 percent of the ground cover on average and was predominantly associated with areas along the transect that were higher in nitrogen and phosphorus. Compilation of the sampling results indicated the magnitude of ground cover was distributed as: blue grama > alkali sacaton > saltgrass > western wheatgrass.

The changes in species composition and ground cover were a function of the rainfall and subsequently available soil water. During years with precipitation greater than 400 mm, a large increase in cover was observed. However, total cover was generally less variable than species composition. The least variable species were blue grama in transects 1 and 3 and saltgrass in transect 2.

Blue grama was positively correlated with the depth of the A horizon, depth to saline soil, and depth of the C horizon as it was found on the sites with the best soil quality and the deepest A horizons. In areas where shallow saline surface horizons existed, saltgrass was the dominant species and total cover was much reduced. Saltgrass responded negatively to nitrogen and positively to an increase in SAR. Alkali sacaton and western wheatgrass were not strongly influenced by salinity, but western wheatgrass was not found on sodic sites, likely due to water stress induced by the soil structure.

1.8.3 Vegetation Associated with Saline-Sodic Soils

Kreeb et al. (1995) conducted an experiment in the Walcha Area, Northern Tablelands in New South Wales to determine if specific vegetative species are associated with saline soils. One 200 m transect was placed along varied terrain: a saline, former swamp area; bare areas interspersed with well-vegetated areas; and uphill, nonsaline grazing land. At each of the 23 sampling sites, the species composition was measured using a 1 m^2 quadrat and soil samples collected from the center of each quadrat. Additional soil samples were also taken at sites where bare areas and vegetation where interspersed.

Cynodon dactylon was present surrounding most of the bare patches and occasionally in small areas within them. In the spring, some *Critesion marinum* was associated with *C. dactylon*, but became dominant at 1 m or more away from the edge of a bare patch. *Festuca elatior* was found as an almost pure stand on the hillside with a large number of herbaceous species.

The soil chemical factors were quite variable along the transect. Soil pH changed suddenly over short distances along the transect, particularly where bare areas occurred. For example, within 2 m, pH changed from 11 to 6.3 from the base of the slope to an up slope area. EC values were low in most areas, except in the bare patches at the soil surface where EC was greater than 1.9 dS/m (analysed using a 1:5

extract), indicating extreme salinity. With increasing depth, the EC declined rapidly at these sites, although pH remained high. The highest SAR value was 20, recorded at an alkaline bare patch. SAR decreased rapidly with depth to parallel the decreasing EC values. Where present, "the alkalinity was due to the presence of strongly dissociated carbonates and/or bicarbonates, notably of Na^{+}" (Kreeb et al. 1995).

Prior to determining if there was a correlation between the soils and vegetation, the vegetation was grouped by the communities in which it was found. The large differences in pH and soil chemistry within and surrounding the bare areas was positively correlated to the type of vegetation present. Vegetation of these areas was confined to tolerant species or suppressed entirely.

1.9 Diversity, Density and Plant Growth on Saline Soils

1.9.1 Diversity and Salt-Affected Soils

A relationship between plant species diversity and salt-affected soils appears to be present. Generally, plant growth becomes affected by the presence of sodium and/or salts when SAR and EC levels exceed critical values of 15 and 4 dS m^{-1}, respectively (Marschner 1986). However, these values are not exact indicators of a species salt tolerance, as salt-tolerance may vary as much as the pH variance tolerated by the *Plantago* species researched by Van Der Aart (1985). The limited research of plant-soil relationships on salt-affected soils prevents a definite comparison of which species would likely be present within a narrow range of SAR and EC values. This type of information may be elusive, given the adaptability of certain species and the variety of other environmental factors to consider.

1.9.1.1 The Dynamic Equilibrium Hypothesis and Salt-Affected Soils

Sodic soils often have limited nutrient availability (Bowman et al. 1985). Therefore, nutrient limitation as a factor in competitive exclusion is a plausible explanation for the lack of species diversity on sodic soils or saline-sodic soils. Huston's (1979) hypothesis that the intense competition for nutrients will lead to low diversity may not be applicable for these soil types as they may be classed as extremely unsuitable substrates. If germination is arrested or emergence impossible for most species due to the soil physical conditions, then low diversity would be

determined by the unsuitable physical characteristics of competing species and not solely by nutrient limitation. If soil conditions improve, the critical threshold growth rate may be crossed and result in a dramatic increase in species diversity until a second threshold is later reached, causing diversity to decline.

1.9.1.2 The Competition Index and Diversity on Salt-Affected Soils

Grime's (1973) diversity and competitive index includes environmental stress as a factor in determining which types of species will dominate an ecosystem. However, since salt-affected soils are present over a long term, they may not be viewed as the periodic environmental stress Grime (1973) described. However, the hypothesis does reflect the results of McGinnies et al. (1976) Bowman et al. (1985) and Kreeb et al. (1995) in that species diversity declines on most salt-affected soils above a threshold level. With increasing environmental stress, species diversity is reduced and limited to the species that have tolerance for the specific conditions (Grime 1973).

1.9.1.3 Environmental Heterogeneity and Salt-Affected Soils

Environmental heterogeneity is a factor in the diversity of plant species in all three field studies as predicted by Levin (1974). Specific species were generally confined to areas where the soil conditions were appropriate for their nutritional and hydrologic requirements and within their tolerance for toxic ions (McGinnies et al. 1976; Bowman et al. 1985; Kreeb et al. 1995). With an increasing variety of soil conditions, the number of species increased accordingly in all three field studies. The density of founder species with limited ability to invade surrounding, heterogeneous patches is also apparent in each of the field studies as the most salt-tolerant species were not found outside of the highly saline patches. Species located in less saline and/or sodic areas seemed to be found in patches with a narrow range of chemical and physical parameters. A comparison of the diversity of an area without salt-affected soils to the diversity found within the three field studies may provide further information as to whether overall diversity is decreased in the salt-affected soil ecosystems due to the more extreme soils.

1.9.2 Density and Salt-Affected Soils

1.9.2.1 Dynamic Equilibrium and Density on Salt-Affected Soils

Low plant density is associated with low population growth rates, produced by a deficiency in one or more essential resources (Huston 1979). This hypothesis can explain the results in each of the three field studies, as density of vegetation located within the high SAR and EC microsites was generally lower relative to surrounding areas with lower SAR and EC values (McGinnies et al. 1976; Bowman et al. 1985; Kreeb et al. 1995). Sodic and saline-sodic soils are usually limiting due to the unavailability of water and nutrients and toxicity of chlorine, sodium and boron (Marschner 1986). A deficiency and/or toxicity may explain the many bare areas present in the most severely affected soils, especially where slickspots were present.

1.9.2.2 Genetic Feedback and Density on Salt-Affected Soils

Shmida and Ellner's (1984) research on intraspecific and interspecific competition may be applicable to areas with salt-affected soils. Interspecific competition may have allowed a species, such as saltgrass, to become a superior competitor on soils with high SAR and EC values, but conversely, other species may not have been able to tolerate this type of substrate and therefore, interspecific competition may not have occurred.

1.9.3 Density and Diversity on Salt-Affected Soils

1.9.3.1 Diversity and Population Densities on Salt-Affected Soils

Huston (1979) examined the relationship between density and diversity. Within a low density community, plant species could potentially mirror the heterogeneity in soils, while within a high density community, species could enter into less preferred soils due to crowding and mask the subtle soil differences. McGinnies et al. (1976) and Kreeb et al. (1995) did not address the relationship between density and diversity, possibly since they only conducted research at the same site for one growing season. Bowman et al. (1985) did analyse the same site for three years and found the species composition within the permanent quadrats did vary, but total cover was less variable. Therefore, species may be entering into areas that are different from their preferred soils, regardless of the change in total density.

1.9.3.2 Diversity and Disturbance on Salt-Affected Soils

Shmida and Ellner (1984) found the removal of competitive species due to a disturbance may allow species from other diverse habitats to enter the community. This hypothesis is probably not valid for salt-affected soils, as species from diverse habitats may not be able to tolerate the extreme substrate conditions.

1.9.3.3 Competitive Exclusion and Density on Salt-Affected Soils

The research conducted by Koch (1974) indicates that population reductions can lessen the chance of competitive exclusion. This research may not be applicable for salt-affected soils since competitive exclusion is apparent due to the nature of the substrate, rather than the growth rates of individual species during different parts of the growing season.

1.9.4 Community Formation on Saline and Sodic Soils

The vegetative patterns discovered in the Colorado studies indicate that saltgrass can be found in microsites where SAR and EC is high (McGinnies et al. 1976; Bowman et al. 1985). By analyzing spatial distributions of vegetation, hypotheses concerning the processes relevant to the formation of the community can be tested (Moloney et al. 1992). Current patterns provide the opportunity to observe the spatial scales over which the processes function, but the patterns are merely static representations of a system. Therefore, pattern analysis is an exploratory tool that may reveal spatial or temporal relationships at different scales.

The assembly rules that govern the formation of patterns are important in understanding how the communities studied by McGinnies et al. (1976), Bowman et al. (1985) and Kreeb et al. (1995) were formed, according to Weiher and Keddy (1995). Why the species composition variability within the permanent quadrats exists when the soils are similar is unknown (Bowman et al. 1985). Research by McGinnies et al. (1976) and Kreeb et al. (1995) indicated that the salt-tolerant species mirrored the changes in soil conditions. Alternatively, Van Der Aart (1985) found two *Plantago* species were able to inhabit a wide variety of habitats with varying soil chemical properties and therefore varying soil physical conditions.

The historical aspect of community formation is an important consideration according to Drake (1991). How certain species become adapted to saline or saline-sodic sites and which species were initially part of these plant communities is unknown. The historical aspect must also consider that soils are not static. If SAR and EC values increased rapidly over time at a particular site, perhaps due to deforestation causing an increase in recharge quantities, then not all species may be able to survive there. Since groundwater containing NaCl is derived from deep, regional flows, a widespread change in the recharge region may alter the quantity of discharge across a large area. This would affect entire plant communities as opposed to microsites and may competitively exclude many members, lowering diversity.

1.10 Research Objectives

The presence of specific plant species at sites with salt-affected soils requires tolerance of a substrate that other species cannot survive on, even without competition, and may produce vegetation patterns that mirror the soil salinity. Species richness and density within the transition zones and surrounding areas appears to provide further evidence of vegetation patterns, but the research is sparse and limited to two small areas: Colorado and New South Wales. Further research involving other ecosystems needs to be conducted to verify the validity and existence of definite vegetation patterns.

The assembly rules that govern the community formation processes remain elusive. Some of the hypotheses presented within this paper seem applicable to areas of salt-affected soils and appear to predict the plant community response to competitors, changes in environmental conditions and disturbance. However, few studies are of a long term nature, like those conducted by Ramenskii (1925) in the early 1900s nor are they specific to species native to the western Canadian Aspen Parkland Ecoregion. More research of this kind is required to determine what assembly rules may be present and how the end point communities evolve.

Restoration of disturbed lands to mimic native ecosystems will be difficult for many reasons. Replication of undisturbed sites is difficult, if not impossible, given the known variables and more importantly, the unknown factors that can alter community development. This makes comparative research challenging and open to be refuted. More formidable and important in the determination of community development, is the

study of the whole ecosystem as opposed to only components of it. However, this is beyond the scope of most researchers. As an alternative, long term research, examining two or three components of an ecosystem in depth, will likely have to suffice.

The following chapters describe research involving the Aspen Parkland Ecoregion of western Canada. Chapter 2 describes the research site and its history as an area for long-term research. Chapter 3 focuses on plant community development. For this research, data were collected during the third and fourth growing seasons to determine if the seeded native plant species and their respective densities in the original seed mix are realized in the plant community. Chapter 4 encompasses research conducted on seeded native grasses and forbs growing in Black Chernozemic and Solonetzic soils with variable levels of salinity to determine if soil salinity, particularly electrical conductivity, produces vegetation patterns. There are two objectives for each research chapter. The general research objective for both chapters is to determine if native plant community assembly processes can be predicted, while the chapter-specific research objectives are to determine if plant species composition and/or density reflects the seed mix during the third and fourth growing seasons and if the seeded plant species composition and/or density is affected by soil salinity.

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CHAPTER TWO
THE RESEARCH SITE

2.0 Research Site

2.1 Site Location and Description

The research site is located within the Aspen Parkland Ecoregion at the Parkland Agricultural Research Initiative (PARI) Conservation Farm, close to Mundare, Alberta, 100 km east of Edmonton (NE and SE quarters of Sec 9, T53, R16, W of the 4th meridian). There are five blocks within the research site: A1, A2, B3, C4 and C5. Refer to Appendix A: Figures A.1, A.2 and A.3 for maps of the research site.

2.1.1 Vegetation

The Aspen Parkland Ecoregion is a transition zone between the drier grasslands to the south and the boreal forests in the north (Strong and Leggat 1981). Clones of aspen are dominant and interspersed with grasslands throughout this region (Moss 1932). The mesic conditions of the Aspen Parkland permit the formation of a lush understory with a diverse mix of shrubs and forbs within the aspen forests (Strong and Leggat 1981). Understory shrub vegetation includes *Rosa acicularis* (wild rose), *Amelanchier alnifolia* (saskatoon), *Symphoricarpos occidentalis* (buckbrush), *Elaeagnus commutata* (silverberry) and *Symphoricarpos albus* (snowberry) (Strong and Leggat 1981). Forbs and grasses present in the understory include *Galium boreale* (northern bedstraw), *Epilobium angustifolium* (fireweed), *Fragaria virginiana* (wild strawberry), *Delphinium glaucum* (larkspur) and *Thalictrum venulosum* (veiny meadow rue) (Strong and Leggat 1981). In the grassland areas, *Festuca hallii* (plains rough fescue), *Agropyron trachycaulum* (slender wheatgrass), *Koeleria macrantha* (June grass), *Agrostis scabra* (rough hair grass), *Oryzopsis asperifolia* (rough-leaved rice grass), *Poa palustris* (fowl bluegrass), *Bromus ciliatus* (fringed brome) and *Schizachne purpurascens* (purple oat grass) are common (Johnson et al. 1995).

2.1.2 Precipitation

The Aspen Parkland receives an average of 450 mm of precipitation each year, with the highest mean monthly precipitation occurring in June and July with 81 mm and

77 mm, respectively (Strong and Leggat 1981). At Vegreville, the closest weather station, the 30 year average annual precipitation is 402.8 mm (Environment Canada 1993). The mean rainfall is 318.4 mm annually with the greatest rainfall occurring during July with 83.2 mm and June with 73.0 mm (Environment Canada 1993). During the winter months, 83.8 cm of snow falls on average, with December and November having the greatest amounts at 17.9 and 12.1 cm respectively. The highest month end snow cover is 24 cm and occurs in February (Environment Canada 1993).

2.1.3 Temperature

The mean temperatures for Vegreville rise above 0 °C in April (3.4 °C) and remain above freezing until October (4.2 °C) (Environment Canada 1993). The highest mean temperature occurs during July at 16.2 °C followed by August at 15.2 °C and June at 14.4 °C. January is the coldest month with a mean average temperature of -16.2 °C. From October through April there are no degree days above 18 °C and conversely, June, July and August are the only months when there are no degree days below 0 °C. Annually, the daily maximum and minimum temperatures are 7.6 and -4.9 °C, respectively. The annual mean is 1.4 °C.

2.1.4 Soils

Black Chernozemic soils, formed under the grassland vegetation are typical, with Dark Gray Chernozems occupying areas where the aspen forests have been established for long periods, causing eluviation (Strong and Leggat 1981). These soils are typically moderately well drained. Chernozemic, Solonetzic and Gleysolic soil groups are mixed within the blocks (Walker 1992). Forty percent of the seeded area contains 70 percent Solonetzic soils, (blocks C:4, C:5) with the remainder of the area composed of 20 to 25 percent Chernozemic soils. Block A:1 and A:2 soils are a Hobbema-Beaver Hills association, composed of 40 to 70 percent Orthic Black Chernozems, 20 to 30 percent Humic Luvic Gleysols and 15 to 20 percent Solonetzic soils as the major soil types. The Solonetzic soils occur randomly on mid-slope to hilltop positions where salts are near the surface. Block B:3 is an Angus Ridge-Norma soil series association. Eluviated Black Chernozems, Solonetzic Black Chernozems and Humic Luvic Gleysols soils each occupy 20 to 30 percent of the area, and gleyed

saline/carbonated soils account for 10 to 20 percent of the remaining major soils. Each of these soils commonly has a saline subsoil. Blocks C:4 and C:5 are of the Camrose-Norma series composed of 30 to 40 percent Black Solodized Solonetzic, 20 to 30 percent Solonetzic Black Chernozems and 15 to 25 percent Humic Gleysols. Saline soils occur on the hilltops to lower slopes, with gleysols occupying the depressional areas. Additional information on the soils at the research site is in Appendix B.

2.2 Research Site Preparation and Seeding

The areas for the research site were randomly chosen within the PARI Farm. Five blocks were randomly selected from a possible twelve blocks. Each block was formerly a tame pasture composed of mainly *Bromus inermis* (smooth brome grass) and *Poa pratensis* (Kentucky bluegrass) that was sprayed with glyphosate at a rate of 3.7 L. per hectare on July 13, 1993 (Kupchenko 1998). A heavy breaking plow was used to break the site on August 16, 1993 and a lighter disk was utilized in August, November and in the spring of the following year. Blocks A:1, A:2 and B:3 were disked and cultivated prior to seeding while C:4 and C:5 were disked and harrow packed. Blocks A1, A2 and B3 were disked and cultivated once more before seeding, while C4 and C5 were cultivated and harrow-packed before seeding (Bush 1998). Species native to the Aspen Parkland were seeded in spring 1994, using six species seed mixes in ten (9.2 x 18.3 m) plots in each of five blocks. Within each block, each treatment was randomly chosen. Four of the six seed mixes have species combinations that were replicated twice, but the density of each of the species was altered to produce a unique treatment. The remaining two mixes were applied at only one seeding rate. Hence, there are ten treatments, each replicated five times for a total of 50 plots. Refer to Appendix B for seed mixes and seeding rates.

On May 30, 1994, blocks A:1, A:2, C:4 and C:5 were seeded, using a Kohler 8 cone seed drill for large seed while the small seeds were hand broadcast with cornmeal (Bush 1998). Wet conditions delayed hand broadcasting for one week after the large seeds were sown and therefore they were not packed into the soil with the seed drill (Bush 1998). Block B:3 was seeded on June 6 using the same seed drill, but the small seeds were broadcast ahead of the seed drill to increase seed-soil contact.

Wind drift may have caused an uneven allocation of seeds on June 6 (Bush 1998). A list of the seeds that were broadcast on all sites is provided in Appendix B.

2.3 *Cirsium arvense* (Canada thistle)

Cirsium arvense (Canada thistle) was common at the A:1 and A:2 blocks during the first and second growing seasons (Bush 1998). Since it is considered a noxious weed and is situated in an agricultural research area, efforts to control it were undertaken. During the 1994 season, glyphosate, hand-picking and digging were utilized to control the species, with additional hand-picking and pulling in the second year. *C. arvense* is still a problem at these blocks. At block C:4, *C. arvense* is prolific in some plots and hand-picking and pulling were conducted in July 1996 to reduce plant vigour.

2.4 Initial Plant Community Development and Management

2.4.1 Soil Sampling and Analysis

Soils data collected in 1994 and 1995 by Bush (1998) were used to characterize the soils at the research site. In June 1994, 3 soil cores were taken from each plot and analysed at 0 to 15 cm and 30 to 40 cm depths for electrical conductivity (EC) and sodium adsorption ratio (SAR). In August 1995, after obtaining EC measurements of the soil located 300 cm east of each quadrat using a Geonics EM38 meter, soil samples were taken using a stratified random sampling method. Using the information obtained from the 1994 lab analysis results and the 1995 EM38 readings, increased soil sampling of up to 5 soil cores was conducted at the most variable plots and one soil core per plot in the saline and non-saline areas was taken where there was less variability (Bush 1998). The soils were analysed using a saturated paste extract (McKeague 1978). The saturation percent is the amount of water (ml) adsorbed by 100 g of dried and ground soil before a sheen of excess water becomes visible. For the results of the 1994 and 1995 soils analyses see Tables 2.1 and 2.2, respectively.

2.4.2 Plant Species Composition and Analysis

Bush (1998) collected plant species data from the research site in July 1994 and July 1995 and analysed the species composition of the plant community in relation to the seed mix to determine if the seeded species density and diversity mirrored the seed mix. Bush (1998) found that the density of *Achillea millefolium, Penstemon procerus, Agropyron trachycaulum/subsecundum, A. riparian, A. dasystachyum, Bromus anomalus* and *Festuca rubra* was relatively high, while *Festuca hallii, Koeleria macrantha, Oenothera biennis, Poa palustris, Rumex occidentalis, Stipa curtiseta, S. viridula, S. comata* and *Bouteloua gracilis* had initially lower densities which declined from 1994 to 1995. The diversity also declined from 1994 to 1995 as *Stipa comata* and *Bouteloua gracilis* were no longer observed within the permanent quadrats.

The analysis of variance (ANOVA) results indicate that *Agropyron trachycaulum* and *A. subsecundum* had the highest relative density (density/pure live seeds using field germination rate test results) followed by *Bromus anomalus, Achillea millefolium* and *Penstemon procerus* (Bush 1998). These five species are considered by Bush (1998) to be early successional species. Some species had significantly higher densities in 1995 than in 1994 (*Achillea millefolium, Agropyron dasystachyum, A. trachycaulum, A. riparian, A. subsecundum* and *Festuca rubra)* possibly due to rhizomatous reproduction or late germination (Bush 1998). Seeds blown in from surrounding mature *Achillea millefolium, A. trachycaulum* and *A. subsecundum* plants may have also increased the plant density of these species (Bush 1998). Conversely, *Koeleria macrantha, Festuca hallii, Oenothera biennis, Stipa curtiseta, S. viridula, S. comata* and *Rumex occidentalis* had lower densities in 1995 compared to 1994, indicating low survivability (Bush 1998).

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Table 2.1 Soil Chemical Characteristics of the Research Site in 1994 Analysed by Saturated Paste Extracts

	A1:1		A1:2		A1:3		A1:4		A1:5	
Depth (cm)	0-15	30-45	0-15	30-45	0-15	30-45	0-15	30-45	0-15	30-45
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	3.5	4.5	4.0	0.6	4.3	1.1	4.1	13.2	3.8	0.9
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	1.6	2.7	1.9	0.5	2.0	0.9	1.1	3.7	2.2	0.7
Na (cmol (Na^{+}) kg^{-1})	0.3	1.2	0.3	1.7	0.3	1.4	0.2	0.9	0.6	11.5
pH	5.8	6.7	5.6	6.0	5.6	6.8	6.7	7.6	5.4	8.0
EC (dS/m)	0.9	1.3	1.1	0.7	1.2	0.7	0.8	2.6	1.2	2.1
Saturation (%)	59.0	52.0	57.0	41.0	56.0	44.0	61.0	48.0	55.0	56.0
SAR	0.2	0.9	0.3	3.6	0.2	2.2	0.1	0.4	0.4	17.4
Organic carbon (%)	5.7	3.4	5.9	1.9	5.5	2.2	4.7	2.1	5.7	0.1
Organic matter (%)	10.1	6.0	10.5	3.5	9.8	3.8	8.4	3.7	10.1	0.2

	A1:6		A1:7		A1:8		A1:9		A1:10	
Depth (cm)	0-15	30-45	0-15	30-45	0-15	30-45	0-15	30-45	0-15	30-45
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	8.5	5.6	3.2	3.8	4.1	1.5	7.3	3.5	3.0	1.1
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	4.4	3.8	1.7	5.5	1.4	0.7	2.6	3.8	1.3	0.7
Na (cmol (Na^{+}) kg^{-1})	2.5	6.4	0.5	13.4	0.2	0.6	0.9	3.5	0.2	0.8
pH	6.4	7.3	5.7	6.5	5.7	6.2	7.0	7.2	5.8	2.8
EC (dS/m)	2.1	2.4	1.0	4.5	0.9	0.6	1.5	1.7	0.7	0.6
Saturation (%)	60.0	52.0	58.0	40.0	63.0	46.0	63.0	48.0	61.0	42.0
SAR	1.2	4.1	0.4	9.8	0.2	0.8	0.5	2.6	0.2	1.2
Organic carbon (%)	5.4	2.7	5.6	1.2	5.3	2.5	4.3	0.7	4.9	1.6
Organic matter (%)	9.7	4.8	9.9	2.1	9.4	4.4	7.7	1.3	8.6	2.8

Table 2.1 Soil Chemical Characteristics of the Research Site in 1994 Analysed by Saturated Paste Extracts (con't)

	A2:1		A2:2		A2:3		A2:4		A2:5	
Depth (cm)	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	2.5	1.0	4.0	8.4	5.5	2.7	1.9	9.4	4.7	11.4
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	1.4	0.9	1.9	9.3	2.6	2.0	1.6	17.4	2.8	15.6
Na (cmol (Na^{+}) kg^{-1})	0.5	2.9	0.5	6.5	0.5	1.7	0.7	19.9	1.3	20.0
pH	6.0	7.4	6.4	7.4	6.9	7.7	6.2	7.7	6.3	7.6
EC (dS/m)	0.7	0.9	0.9	3.3	1.1	1.1	0.7	7.0	1.1	6.2
Saturation (%)	60.0	46.0	72.0	50.0	69.0	45.0	62.0	44.0	73.0	52.0
SAR	0.4	4.5	0.4	3.1	0.3	1.6	0.7	8.2	0.8	7.5
Organic carbon (%)	4.7	1.5	6.5	1.4	4.4	1.4	4.5	0.5	7.1	2.1
Organic matter (%)	8.4	2.6	11.6	2.6	7.7	2.4	8.0	0.8	12.7	3.8

	A2:6		A2:7		A2:8		A2:9		A2:10	
Depth (cm)	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	3.1	4.1	6.3	13.7	3.0	9.4	3.4	3.8	5.2	13.1
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	2.1	5.7	1.9	6.2	2.4	23.0	2.3	5.9	1.7	21.1
Na (cmol (Na^{+}) kg^{-1})	0.8	9.5	0.3	5.9	1.1	27.9	0.8	10.6	1.5	27.4
pH	5.6	7.4	6.9	7.5	6.2	7.6	6.1	7.6	7.1	7.8
EC (dS/m)	1.0	3.4	1.1	3.7	0.9	8.0	1.0	3.4	1.0	7.1
Saturation (%)	63.0	45.0	72.0	48.0	66.0	47.0	61.0	46.0	69.0	54.0
SAR	0.6	6.4	0.2	2.7	0.8	10.1	0.6	7.1	0.9	9.0
Organic carbon (%)	4.9	0.8	4.7	2.1	6.7	1.4	5.3	1.4	5.4	2.5
Organic matter (%)	8.7	1.5	8.4	3.7	11.9	2.4	9.5	2.5	9.5	4.5

Table 2.1 Soil Chemical Characteristics of the Research Site in 1994 Analysed by Saturated Paste Extracts (con't)

	B3:1		B3:2		B3:3		B3:4		B3:5	
Depth (cm)	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	4.6	3.4	3.1	1.2	3.4	0.8	7.1	6.7	4.1	1.4
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	1.8	1.4	1.5	0.8	1.5	0.5	0.2	4.2	1.8	0.1
Na (cmol (Na^{+}) kg^{-1})	0.3	1.2	0.3	0.5	0.3	0.8	0.4	3.2	0.3	0.7
pH	6.4	7.6	6.1	7.5	5.9	6.4	6.7	7.6	6.2	7.6
EC (dS/m)	1.0	1.0	0.8	0.5	0.8	0.5	1.1	2.4	0.9	0.6
Saturation (%)	63.0	50.0	67.0	40.0	66.0	47.0	76.0	44.0	67.0	40.0
SAR	0.2	1.0	0.2	0.8	0.3	1.4	0.2	2.1	0.2	1.0
Organic carbon (%)	6.0	1.7	5.6	0.9	5.4	2.3	6.4	1.7	5.3	1.3
Organic matter (%)	10.7	3.1	10.0	1.6	9.5	4.1	11.4	3.0	9.4	2.4

	B3:6		B3:7		B3:8		B3:9		B3:10	
Depth (cm)	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	2.7	0.4	3.0	0.5	4.6	0.7	3.5	3.2	3.3	3.6
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	1.3	0.2	1.7	0.3	0.6	0.4	1.5	2.2	1.6	3.2
Na (cmol (Na^{+}) kg^{-1})	0.4	0.6	0.4	0.5	0.3	0.9	0.2	1.9	0.3	3.5
pH	5.9	6.9	5.8	6.6	6.5	7.3	6.4	7.7	6.3	7.6
EC (dS/m)	0.7	0.3	0.9	0.4	1.0	0.5	0.8	1.5	0.7	2.1
Saturation (%)	64.0	40.0	59.0	37.0	62.0	39.0	67.0	40.0	72.0	40.0
SAR	0.4	1.8	0.3	1.3	0.2	2.0	0.2	1.8	0.2	3.0
Organic carbon (%)	5.3	0.4	4.9	0.7	4.9	1.0	4.8	0.8	6.3	0.1
Organic matter (%)	9.5	0.8	8.8	1.2	8.6	1.8	8.6	1.5	11.3	0.2

Table 2.1 Soil Chemical Characteristics of the Research Site in 1994 Analysed by Saturated Paste Extracts (con't)

	C4:1		C4:2		C4:3		C4:4		C4:5	
Depth (cm)	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	3.5	0.4	1.2	3.0	1.6	1.7	4.1	3.5	4.6	0.9
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	1.9	0.2	1.0	4.2	1.2	2.7	1.3	1.1	2.1	0.5
Na (cmol (Na^{+}) kg^{-1})	1.1	1.3	7.0	29.5	3.7	20.8	0.2	0.3	0.2	0.3
pH	5.7	6.4	6.9	8.0	5.2	6.7	7.1	7.3	5.9	6.1
EC (dS/m)	1.0	0.5	1.3	4.9	1.1	4.7	1.0	0.9	1.1	0.3
Saturation (%)	69.0	43.0	58.0	63.0	59.0	43.0	48.0	45.0	61.0	43.0
SAR	0.8	3.6	8.9	19.5	4.1	21.2	0.2	0.3	0.2	0.5
Organic carbon (%)	4.4	0.7	3.4	0.5	4.3	0.5	3.1	2.2	4.7	0.5
Organic matter (%)	7.8	1.3	6.0	0.8	7.6	0.9	5.5	3.9	8.3	0.9

	C4:6		C4:7		C4:8		C4:9		C4:10	
Depth (cm)	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	3.3	0.8	4.4	1.9	1.8	1.9	1.6	9.3	3.2	1.2
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	1.7	0.3	1.6	0.6	0.8	1.1	1.2	12.4	1.7	0.7
Na (cmol (Na^{+}) kg^{-1})	2.1	3.4	0.7	0.6	0.9	1.0	5.3	64.0	0.2	0.3
pH	5.2	6.4	6.9	7.4	7.3	5.9	5.1	7.4	6.1	6.3
EC (dS/m)	1.2	0.9	1.0	0.7	0.6	0.8	1.5	8.8	0.9	0.5
Saturation (%)	59.0	43.0	56.0	40.0	41.0	51.0	54.0	69.0	56.0	39.0
SAR	1.7	7.3	0.5	0.9	1.1	1.2	6.1	23.4	0.1	0.4
Organic carbon (%)	5.1	0.6	2.7	0.2	0.8	4.0	4.2	0.4	4.8	1.3
Organic matter (%)	9.0	1.0	4.8	0.4	1.4	7.1	7.4	0.7	8.47	2.3

Table 2.1 Soil Chemical Characteristics of the Research Site in 1994 Analysed by Saturated Paste Extracts (con't)

	C5:1		C5:2		C5:3		C5:4		C5:5	
Depth (cm)	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	0.8	13.2	1.0	1.5	0.5	11.1	2.7	1.6	1.3	12.0
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	0.6	15.6	0.7	1.6	0.4	14.8	1.8	1.4	1.5	14.0
Na (cmol (Na^{+}) kg^{-1})	8.4	73.9	3.7	9.1	5.5	77.4	3.7	30.2	8.8	61.6
pH	5.5	7.9	6.2	6.8	5.2	7.3	5.1	7.2	5.2	7.7
EC (dS/m)	1.6	11.6	1.0	2.0	1.0	9.7	1.2	5.5	2.0	11.1
Saturation (%)	59.0	56.0	46.0	50.0	57.0	71.0	60.0	47.0	56.0	57.0
SAR	13.0	26.1	5.9	10.3	10.5	25.4	3.1	36.0	9.9	22.6
Organic carbon (%)	4.0	0.2	2.5	1.0	3.9	0.6	5.0	0.8	4.6	0.5
Organic matter (%)	7.1	0.3	4.4	1.7	6.9	1.0	9.0	1.4	8.2	0.9

	C5:6		C5:7		C5:8		C5:9		C5:10	
Depth (cm)	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm	0-15 cm	30-45 cm
Ca (cmol (1/2 Ca^{2+}) kg^{-1})	1.9	0.9	0.6	0.7	4.4	1.4	1.4	9.8	2.9	1.3
Mg (cmol (1/2 Mg^{2+}) kg^{-1})	1.7	1.7	0.5	0.4	3.1	1.1	1.0	7.6	1.1	0.6
Na (cmol (Na^{+}) kg^{-1})	6.2	32.9	4.9	4.3	2.9	15.0	4.4	51.9	0.6	0.3
pH	7.1	8.6	6.0	7.6	5.3	6.7	5.3	6.3	6.8	7.5
EC (dS/m)	1.6	4.0	1.5	0.9	1.9	2.9	1.1	8.0	0.9	0.6
Saturation (%)	57.0	78.0	40.0	56.0	65.0	54.0	65.0	70.0	47.0	36.0
SAR	6.1	33.2	10.5	7.6	1.9	18.6	4.9	21.0	0.6	0.5
Organic carbon (%)	4.3	0.7	1.6	0.1	6.7	1.2	5.8	0.7	2.2	0.1
Organic matter (%)	7.6	1.3	2.9	0.1	11.9	2.2	10.0	1.3	4.0	0.2

Table 2.2 Sodium Analysis of the Soils at the Research Site, 1995 Analysed by Saturated Paste Extract

Block:Treatment	A1:1	A1:2	A1:3	A1:5						A1:6
Quadrat	11:7	15:3	3:6	11:4	13:7	17:2	18:3	19:2	8:5	9:3
Na (cmol (Na^+) kg^{-1})	0.4	0.2	0.2	0.3	0.4	0.3	0.4	0.3	0.4	0.2
Saturation (%)	62	64	63	61	61	56	57	52	63	61

Block:Treatment	A1:7						A1:8	A1:9	A1:10
Quadrat	16:4	17:8	18:4	5:8	8:6	9:6	16:5	12:2	15:7
Na (cmol (Na^+) kg^{-1})	0.4	0.4	0.5	0.2	0.3	0.2	0.1	0.4	0.1
Saturation (%)	57	55	56	57	57	57	56	58	56

Table 2.2 Sodium Analysis of the Soils at the Research Site, 1995. Analysed by Saturated Paste Extract (con't)

Block:Treatment	A2:1			A2:2			A2:3			
Quadrat	13:7	16:3	6:3	19:7	5:8	5:9	13:4	18:7	2:3	3:7
Na (cmol (Na^+) kg^{-1})	0.4	0.3	0.4	0.6	0.4	0.2	0.4	0.3	0.1	0.1
Saturation (%)	56	57	63	63	69	69	56	62	60	61

Block:Treatment	A2:3		A2:4						A2:5	
Quadrat	8:4	9:4	14:9	15:8	17:7	2:2	2:8	6:5	12:6	15:3
Na (cmol (Na^+) kg^{-1})	0.2	0.2	0.5	0.3	0.6	0.5	0.5	0.6	0.5	0.4
Saturation (%)	55	56	64	55	57	61	60	58	66	68

Block:Treatment	A2:5				A2:6					
Quadrat	18:7	3:7	4:7	8:3	10:6	11:6	12:6	4:6	4:8	7:6
Na (cmol (Na^+) kg^{-1})	0.5	0.4	0.7	0.7	0.9	0.7	0.6	0.4	0.4	0.6
Saturation (%)	75	71	76	69	59	58	62	64	64	60

Block:Treatment	A2:7		A2:8						A2:9	
Quadrat	12:8	19:2	14:4	14:8	18:6	4:2	5:6	7:8	12:9	13:8
Na (cmol (Na^+) kg^{-1})	0.3	0.2	1.9	1.2	0.6	0.5	0.3	0.3	0.5	0.5
Saturation (%)	64	64	64	68	63	66	67	71	64	63

Table 2.2 Sodium Analysis of the Soils at the Research Site, 1995. Analysed by Saturated Paste Extract (con't)

Block:Treatment	A2:9				A2:10					
Quadrat	14:4	3:3	6:2	8:7	11:6	13:5	13:8	16:4	3:6	6:9
Na (cmol (Na^+) kg^{-1})	0.5	0.5	0.3	0.4	0.8	0.7	0.7	0.6	0.3	0.5
Saturation (%)	62	58	56	64	63	64	70	69	62	67

Block:Treatment	B3:1	B3:2	B3:3	B3:4	B3:5	B3:6	B3:7	B3:8	B3:9	B3:10
Quadrat	6:6	10:8	12:3	15:9	14:2	13:5	15:2	16:8	8:7	10:6
Na (cmol (Na^+) kg^{-1})	0.2	0.1	0.3	0.3	0.1	0.1	0.3	0.2	0.2	0.2
Saturation (%)	73	66	68	72	63	66	65	62	70	70

Table 2.2 Sodium Analysis of the Soils at the Research Site, 1995. Analysed by Saturated Paste Extract (con't)

Block:Treatment	C4:1		C4:2							C4:3
Quadrat	11:4	18:7	4:2	12:8	15:2	15:3	16:4	18:2	4:2	12:6
Na (cmol (Na^+) kg^{-1})	0.1	0.6	0.6	0.3	0.4	0.1	1.4	1.1	0.7	0.8
Saturation (%)	55	62	66	55	64	56	60	73	60	48

Block:Treatment	C4:3					C4:4	C4:5	C4:6		
Quadrat	15:2	15:9	16:7	19:4	5:6	6:8	10:4	11:4	16:5	19:5
Na (cmol (Na^+) kg^{-1})	1.2	2.7	2.3	2.2	0.2	0.0	0.1	0.6	0.4	1.8
Saturation (%)	51	48	49	51	57	47	57	58	56	59

Block:Treatment	C4:6			C4:7			C4:8		C4:9	
Quadrat	3:3	4:8	6:2	14:9	3:3	8:4	10:5	18:8	10:3	10:6
Na (cmol (Na^+) kg^{-1})	0.3	1.1	0.4	1.0	0.2	0.3	0.2	0.1	3.2	2.7
Saturation (%)	60	60	59	51	55	55	45	48	56	59
	0.52	1.77	0.76	1.9	0.31	0.48	0.35	0.13	5.79	4.54

Block:Treatment	C4:9				C4:10
Quadrat	11:4	14:5	17:9	6:5	4:6
Na (cmol (Na^+) kg^{-1})	2.4	2.6	0.4	3.1	0.1
Saturation (%)	57	50	53	69	53

Table 2.2 Sodium Analysis of the Soils at the Research Site, 1995. Analysed by Saturated Paste Extract (con't)

Block:Treatment	C5:1						C5:2			
Quadrat	13:3	18:4	19:8	2:6	5:9	9:8	15:2	16:9	19:2	2:6
Na (cmol (Na^+) kg^{-1})	6.3	7.6	3.9	4.8	2.8	4.0	0.4	9.0	1.6	0.2
Saturation (%)	58	59	61	61	70	65	60	58	53	51

Block:Treatment	C5:2		C5:3						C5:4	
Quadrat	4:6	8:6	10:5	13:9	14:5	16:2	6:8	7:5	16:4	3:5
Na (cmol (Na^+) kg^{-1})	0.3	0.4	3.9	3.4	3.9	3.0	2.4	3.3	19.8	2.2
Saturation (%)	50	46	51	56	52	60	52	54	56	58

Block:Treatment	C5:4			C5:5						C5:6
Quadrat	5:3	8:6	9:4	10:5	14:9	19:7	4:8	7:9	9:8	10:3
Na (cmol (Na^+) kg^{-1})	1.1	0.6	0.7	6.0	2.7	4.4	3.9	0.8	0.8	4.1
Saturation (%)	67	63	62	58	73	71	58	58	60	73

Block:Treatment	C5:6				C5:7			C5:8		
Quadrat	11:4	15:2	17:7	18:8	10:2	11:4	12:5	12:8	16:7	2:5
Na (cmol (Na^+) kg^{-1})	0.8	5.1	0.4	0.6	1.3	1.1	1.0	2.0	3.3	2.5
Saturation (%)	62	74	69	69	51	57	50	75	76	68

Table 2.2 Sodium Analysis of the Soils at the Research Site, 1995. Analysed by Saturated Paste Extract (con't)

Block:Treatment	C5:8			C5:9						C5:10
Quadrat	6:6	7:6	8:5	10:7	14:2	16:7	17:2	2:2	6:2	11:2
Na (cmol (Na^+) kg^{-1})	3.3	3.3	3.7	0.5	0.9	0.5	2.4	4.7	4.3	0.6
Saturation (%)	72	72	76	74	77	73	73	75	71	56

Block:Treatment	C5:10	
Quadrat	12:5	18:6
Na (cmol (Na^+) kg^{-1})	0.5	1.0
Saturation (%)	55	55
	0.94	1.82

CHAPTER 3
PLANT COMMUNITY DEVELOPMENT IN ALBERTA ASPEN PARKLAND

3.1 Introduction

Ecosystems are communities of organisms and their physical environment interacting as an ecological unit (Lincoln et al. 1982). Plant communities within an ecosystem interact through energy flows, element cycling and by modifying the microsites within the system. The diversity and density of plant species within an ecosystem varies temporally and spatially. Understanding the relationships between the structure of plant communities and how they function is a key goal of ecology through identification and quantification of plant species (McCormick et al. 1974).

3.1.1 Plant Community Assembly Processes

Assembly processes relate to how plant species are formed into plant communities over time. The important influences on succession have been discussed among several researchers and there are many differing opinions on which assembly processes have scientific merit.

Wilson (1992) believes communities are composed of spatially heterogeneous mosaic patches that are fragments of much larger ecosystems, known as metacommunities. Within communities, many complex interactions occur among species which result in community patterns. These complex interactions are difficult to predict and may appear chaotic. One common feature of complex interactions, chaotic and otherwise, is sensitive dependence on initial conditions, in which small perturbations will have large effects on the outcome of deterministic interactions (Wilson 1992).

Competition for resources is commonly cited as a significant assembly process. Diamond's (1975) research indicates an ability to resist the invasion of a new species as one reason that adjacent plant communities with similar habitats often do not contain the same species. A second reason may be in the existing community's ability to use available resources optimally, thereby reinforcing the ability of the community to resist invasion of plant species (Diamond 1975). Tilman (1982) believes that competition among plant species for inorganic nutrients influences community

structure. Communities that become enriched with nutrients often have significantly less diversity and the nutrient that is enriched becomes the overriding factor in determining which species achieves dominance (Tilman 1982). Additionally, Tilman (1982) believes the distribution of plant nutrients within a landscape closely correlates with the spatial and temporal distribution of plant species in a landscape.

Levin (1994) also believes the spatial distribution of plant species can be attributed to a heterogeneous landscape and that species diversity is positively correlated with increased environmental heterogeneity. Spatial components of the environment generally operate to increase species diversity since the environment is heterogeneous. Colonization of patches by founder species produces a variety of species mixes in unique proportions which will evolve differently from neighboring patches. Although an increase in species diversity is due to heterogeneous patches, the existence of several types of patches will reinforce the degree of species richness, but does not depend on the presence of several types of patches.

A theory proposed by Pickett et al. (1987) incorporates all of the factors previously discussed as mechanisms of succession. Pickett et al. (1987) have developed a model of succession incorporating all causes of succession in a complete mechanistic scheme. The model entails a variety of endpoints for a community to develop towards and does not have a single or dominant mechanism or driving force while being applicable to many ecosystems. Instead, it relies on the premise that the availability of open sites is a prerequisite for succession to commence and that different species are available for moving onto that site. The species at a particular site have unique, evolved or enforced capabilities to deal with that site and the competition provided by the other species present. "The organism- and site-specific features are responsible for the great variety in the successions we observe" (Pickett et al. 1987).

3.1.2 End Point Communities

Researchers have discovered that end point communities can vary greatly, even if seemingly identical initially. In experiments, community ecologists discovered the replicates of treatments were as different in magnitude as the differences between the treatments (Hurlbert 1984). The subsequent interactions magnified these very small initial differences and provided evidence towards the sensitivity of the

communities (Wilson 1992). Predation and competition are mechanisms that influence the end points of ecological communities and are thought to be well understood for some ecotypes (Drake 1991). However, inconsistencies result when using these processes to predict outcomes with similar community types: patterns can vary between systems that have the same species composition and interspecific interactions.

3.2 Research Objectives and Hypothesis

3.2.1 Research Objectives

The general research objective is to determine if native plant community assembly processes can be predicted. Specifically, the objective is to determine if plant species composition and/or density is consistent among treatment replicates and reflects the density and diversity of the species within the seed mix.

The literature on plant community development contains few field studies to monitor plant community development and community assembly processes. Most field studies are focused on established plant communities or are purely theoretical and therefore, little is known about whether a plant community reflects the seed mix after three and four growing seasons. This is important in land reclamation where seed mixes are carefully designed to form specific plant communities, but whether the plant community develops into an identical or similar species mix and species density is unknown.

3.2.2 Hypothesis

Plant community development is a random process that alters the density and diversity of a plant species on a microsite level.

3.3 Experimental Design and Methods

3.3.1 Site Description

The research site is located within the Aspen Parkland Ecoregion at the Parkland Agricultural Research Initiative (PARI) Conservation Farm, close to Mundare, Alberta, 100 km east of Edmonton (NE and SE quarters of Sec 9, T53, R16, W of the 4th meridian). There are five blocks at the research site: A1, A2, B3, C4 and C5

(Appendix A: Figures A.1, A.2 and A.3). Clones of aspen are dominant and interspersed with grasslands throughout this region (Moss 1932).

The mean rainfall is 318.4 mm annually with the greatest rainfall occurring during July (83.2 mm) and June (73.0 mm) (Environment Canada 1993). During the winter months, 83.8 cm of snow falls on average (Environment Canada 1993).

The mean temperatures rise above 0 °C in April (3.4 °C) and remain above freezing until October (4.2 °C) (Environment Canada 1993). The highest mean temperature occurs during July at 16.2 °C followed by August at 15.2 °C and June at14.4 °C. June, July and August are the only months when there are no degree days below 0 °C. The annual mean is 1.4 °C.

Black Chernozemic soils, formed under the grassland vegetation are typical, with Dark Gray Chernozems occupying areas where the aspen forests have been established for long periods, causing eluviation (Strong and Leggat 1981). These soils are typically moderately well drained.

Chernozemic, Solonetzic and Gleysolic soils groups are mixed within blocks (Walker 1992). Block A:1 and A:2 soils are a Hobbema-Beaver Hills association, with the major soils composed of 40 to 70 percent Orthic Black Chernozems, 20 to 30 percent Humic Luvic Gleysols and 15 to 25 percent Solonetzic soils. The Solonetzic soils occur randomly on mid-slope to hilltop positions where salts are near the surface. Block B:3 is an Angus Ridge-Norma soil series association. Eluviated Black Chernozems, Solonetzic Black Chernozems and Humic Luvic Gleysols soils each occupy 20 to 30 percent of the area, and gleyed saline/carbonated soils account for 10 to 20 percent of the remaining major soils. Each of these soils commonly has a saline subsoil. Blocks C:4 and C:5 are of the Camrose-Norma series composed of 30 to 40 percent Black Solodized Solonetz, 20 to 30 percent Solonetz Black Chernozem and 15 to 25 percent Humic Gleysol. Saline soils occur on the hilltops to lower slopes, with gleysols occupying the depressional areas. Additional information on the soils at the research site is in Appendix B.

3.3.1 Site History

The areas for the research site were randomly chosen within the PARI Farm. Five blocks were randomly selected from a possible twelve blocks. Each block was

formerly a tame pasture composed mainly of *Bromus inermis* and *Poa pratensis* that was sprayed with glyphosate at a rate of 3.7 L per hectare on July 13, 1993 (Kupchenko 1998). A heavy breaking plow was used to break the site on August 16, 1993 and a lighter disk was utilized later in August and November and in the spring of the following year. Blocks A1, A2 and B3 were disked and cultivated once more before seeding, while C4 and C5 were cultivated and harrow-packed before seeding (Bush 1998). Species native to the Aspen Parkland were seeded in spring 1994, using six species seed mixes in ten (9.2 x 18.3 m) plots in each of five blocks. Within each block, each treatment was randomly chosen. Four of the six seed mixes have species combinations that were replicated twice, but the density of each species was altered to produce a unique treatment. The remaining two mixes were applied at only one seeding rate. Hence, there are ten treatments, each replicated five times for a total of 50 plots. Refer to Appendix B for common names, seed mixes and seeding rates.

Bush (1998) collected plant species data from the research site in July 1994 and July 1995 and analysed the composition of the plant community in comparison to the seed mix to determine if the seeded species density and diversity mirrored the seed mix. The analysis of variance (ANOVA) results indicate that *Agropyron trachycaulum* and *A. subsecundum* had the highest relative density (density/pure live seeds using field germination rate test results) followed by *Bromus anomalus, Achillea millefolium* and *Penstemon procerus* (Bush 1998). These five species are considered by Bush (1998) to be early successional species. Some species had significantly higher densities in 1995 than in 1994 (*Achillea millefolium, Agropyron dasystachyum, A. trachycaulum, A. riparian, A. subsecundum* and *Festuca rubra)* possibly due to rhizomatous reproduction or late germination. Seeds blown in from surrounding mature *Achillea millefolium, A. trachycaulum* and *A. subsecundum* plants may have also increased the plant density of these species. Conversely, *Koeleria macrantha, Festuca hallii, Oenothera biennis, Stipa curtiseta, S. viridula, S. comata* and *Rumex occidentalis* had lower densities in 1995 compared to 1994, indicating low survivability.

3.3.2. Vegetation Data Collection

A species composition assessment of the plant species present and measurement of each species respective density was done annually in late July, using five hundred 0.1 m^2 (10 x 50 cm) permanent quadrats. Use of permanent quadrats

allows for yearly changes in vegetation to be attributed to succession or other factors as opposed to variation in the sampling location.

In 1994, after the site was seeded, ten randomly placed, permanent quadrat markers were placed within each plot. Each marker consisted of four spikes and four washers, spray painted a bright colour, which were inserted flush into the soil to indicate where the corners of the quadrat should be aligned. All quadrats were aligned lengthwise north/south in the A1, A2 and B3 blocks and in the C4 and C5 blocks they were aligned east/west. Randomly generated numbers were used to indicate the coordinate positions for the quadrats which were measured by pacing. Prior to conducting the vegetation assessment in the third and fourth growing seasons, the spikes and washers were located by pacing to the coordinates or by use of a metal detector.

In each quadrat, each plant species was identified. After each species was identified, the plant specie's density was assessed by counting the individual plants of that species. Given the difficulty of determining if a plant was a tiller of the parent plant, all species members were counted as individual plants. The density of each seeded species within each treatment plot is in Table 3.1.

3.3.4 Statistical Analysis

SPSS was the statistical software used for each of the following analysis. A p-value less than 0.05 is sufficient to reject the null hypothesis in each of the following analyses (Yeh 1998).

3.3.4.1 Chi Square Analysis of Species Diversity Within Individual Quadrats

Species diversity was analysed by counting the number of seeded species within each quadrat and performing a Chi Square analysis to determine if the differences in the number of species within each treatment plot were statistically significantly different.

3.3.4.2 Chi Square Analysis of Species Diversity Among Treatment Replicates

Species diversity was analysed by using a Chi Square analysis to determine if the species diversity is consistent among each of the five replicates of each treatment for each year.

3.3.4.3 Ranking Analysis for Seed Quantity versus Plant Density Within Plots

A ranking analysis was performed to determine if the proportion of seeds for each species within each treatment per m^2 produced the same proportion of plant species within the seeded plant community. For this analysis, the plant counts of *A. trachycaulum* and *A. subsecundum* were combined as seeding problems in 1994 led to the mixing of the two species and the seed density for the two species is stated by Bush (1998) as one value.

3.3.4.4 Ranking Analysis of Statistically Significant Treatments

Based on the results of the initial ranking test, a second analysis was conducted to compare the total plant counts of the treatments which had consistent p-values of less than 0.05 to the other treatments which contained the six core seeded species. This was done for both years of the data collection and includes the six core seeded species that are present in eight of the ten treatments.

3.3.4.5 Chi Square Analysis of Seeded Species Density Within Quadrats

To determine if the total number of seeded plants within each permanent quadrat is relatively consistent, a Chi Square analysis was conducted.

3.3.4.6 Chi Square Analysis of Seeded Species Evenness Within Each Plot

To determine if the total number of each seeded species is equally represented within a plot, a Chi Square analysis was performed. For this analysis, *Agropyron trachycaulum* and *A. subsecundum* were counted together as one species.

3.3.4.7 Chi Square Analysis of Species Density Among Treatment Replicates

To determine if the density of each seeded species is statistically significantly different among treatment replicates, a Chi Square analysis was performed. Chi Square p-values are additive and the test results from each treatment for each species were added to provide a total Chi Square p-value and a mean of the p-value.

3.3.4.8 Proportion Analysis of the Density of Individual Species

To determine if the density of each seeded species has changed in proportion to the total number of seeded species between 1996 and 1997, a proportion analysis was conducted. This analysis is used to determine if the quantity of a seeded species has changed from 1996 to 1997 and if the proportions are maintained in relation to the total number of seeded species. The null hypothesis would not be rejected for this analysis if the ratio or number of standard errors is less than 2.0. The ratio value is analogous to the probability of occurrence, which at a ratio of 2.0, is 5.74 percent. A probability of 5.74 percent or greater is considered to be statistically significant (Yeh 1998).

3.4 Results and Discussion

3.4.1 Species Diversity Within Individual Quadrats

The number of plant species within permanent quadrats for individual treatment plots were not statistically significantly different in 1996 or 1997. This indicates the number of species within the permanent quadrats is relatively consistent and may indicate that the same species are commonly found within the quadrats. The species diversity within most permanent quadrats is typically three or four species. The Chi Square results are presented in Table 3.2.

3.4.2 Species Diversity Among Treatment Replicates

The species diversity among treatment replicates is not statistically significant for any treatment in 1996 and 1997. This would indicate that the number of species found within the permanent quadrats among the treatment replicates is relatively consistent.

A review of the data shows the same species are consistently present within most of the permanent quadrats and that other species are regularly absent. Of the six species common to eight treatments, also referred to as the core species, the species consistently present within the permanent quadrats includes *Agropyron trachycaulum, A. smithii* and *Bromus anomalus*. *A. subsecundum* was more common in 1996 than 1997. Of the remaining six core species, *Festuca hallii* is present occasionally and *Stipa curtiseta* is typically not present. The species that were seeded in addition to the core species also have members that are typically present or not. Those generally present within the permanent quadrats include *Achillea millefolium* and *Poa palustris*, while those generally absent include *Stipa comata, S. viridula, Koeleria macrantha, Oxytropis deflexa, O. splendens, Oenothera biennis* and *Rumex occidentalis*.

The species unique to the two remaining treatments are also typically present or absent. Those species found consistently within Treatment 10 in 1996 and 1997 include *Agropyron dasystachyum, A. smithii* and *Stipa viridula*. *Medicago sativa* was found in only three quadrats in 1996 and was absent in 1997. In Treatment 5, *Agropyron riparian, A. trachycaulum, Festuca hallii, F. rubra* and *Poa alpina* were always found within the treatment. *Koeleria macrantha* and *Festuca ovina* were found sporadically in some treatment plots and usually at low densities. Data for this analysis can be found in Table 3.3.

3.4.3 Seed Quantity versus Plant Density Within Plots

Seventy percent of the treatments had plant communities which maintained the relative proportions of the seed mix. Three treatments (Treatments 2, 7 and 10) in both 1996 and 1997 had statistically significant differences in the relative rankings of the seed mix to the plant community and with the exception of *Medicago sativa*, all the species in the three treatments were grass species. The plant communities in the three treatments may not resemble the proportions of the seed mix for a variety of reasons.

Treatments 2 and 7 contain the same species but in different proportions. The species for these two treatments include the six core species as well as *Bromus cilatus, Koeleria macrantha, Poa palustris, Stipa comata* and *S. viridula*. The results of the analyses for Treatments 2 and 7 may be poorly correlated to the seed mix due to

the poor germination and/or survival of *Stipa comata, Koeleria macrantha* and *Bromus ciliatus* in all treatments at the research site. Both *S. comata* and *K. macrantha* were seeded at fairly high rates in Treatment 2 but in Treatment 7, *K. macrantha* seed was the third highest quantity and *S. comata* was the third lowest. Poor germination and/or survival of a heavily seeded species could lower the correlation to the entire seed mix.

In addition, the quantity of *Poa palustris* within the permanent quadrats of all treatments is generally high and it may have been in the seed bank as it is commonly found in other treatments where it was not seeded. Therefore, the true contribution of the *P. palustris* seeds within the seed mix to the plant community may be overstated.

Plant communities in Treatment 10 replicates did not reflect the species proportions in the seed mix. *Medicago sativa* was absent in most treatment plots in 1996 and 1997, but it was also seeded at the lowest rate. *Stipa viridula* was the third highest species within the seed mix, but it did poorly in most Treatment 10 plots and the remaining plots on the research site. Data derived from these analyses are in Table 3.4.

3.4.4 Significant Treatments in Section 3.4.3 versus Remaining Treatments

The six core grass species of Treatments 2 and 7 were ranked against the six core grass species in the remaining six treatments to determine if Treatments 2 and 7 were different. This was not possible with Treatment 10 since it did not contain the six core grass species. In 1996 and 1997, the plant counts in Treatments 2 and 7 were highly correlated to those in the other six treatments. These findings indicate that the individual plant densities are relatively consistent, regardless of the treatment. Table 3.5 presents the data for these analyses.

3.4.5 Seeded Species Density Within Quadrats

The results of this analysis indicate the total number of seeded plants within each quadrat is not relatively equal and some quadrats have significantly higher quantities of seeded plants than other quadrats within the same treatment plot. All treatments have at least three replicates that are statistically significantly significant, except for Treatment 6 which has only two statistically significant treatments. In terms of plots, the number of plots that had statistically significant differences in density increased from 28 of 50 in 1996 to 40 of 50 in 1997.

The densities of seeded plants were more evenly distributed within the quadrats in 1996 than in 1997, indicating the density of plant communities at the research site is becoming more variable within the permanent quadrats. The results of these analyses are presented in Table 3.6.

3.4.6 Seeded Species Evenness Within Each Plot

Some species are consistently more prevalent within the plant permanent quadrats and possibly within the plant community. The data from 1996 to 1997 may indicate the dominant seeded species are becoming more dominant within the permanent quadrats or that other species are decreasing. The results of this analysis are presented in Table 3.7.

3.4.7 Species Density Among Treatment Replicates

Many plant densities were statistically significantly different in 1996 and the number increased in 1997. In 1996, twelve analyses could not be performed as the plant densities were zero for six species within some treatments and in 1997, 13 analyses could not be performed for the same reason, indicating that the absent plant species are not reappearing and that a trend to less diversity may be occurring.

Agropyron smithii and *A. subsecundum* were seeded in all ten treatments and in 1996, the quantities of *A. smithii* were statistically significantly different in seven treatments. By 1997, this had increased to nine treatments, indicating that the densities of *A. smithii* are becoming more variable within each of the nine treatments and are remaining relatively consistent in only one treatment, Treatment 5. *A. subsecundum*, in 1996, had quantities that were statistically significantly different in five treatments, but by 1997, this had increased to six treatments indicating that the density of this species within treatments is also becoming more variable with time.

Six core grass species were common to eight of the ten treatments: *Agropyron smithii, A. subsecundum, A. trachycaulum, Bromus anomalus, Festuca hallii* and *Stipa curtiseta*. In 1996 and 1997, *B. anomalus* was the only species found in quantities that were statistically significantly different in all eight treatments, indicating densities of this species are consistently highly variable. In 1996, of the remaining species, the following had statistically significantly different densities (the corresponding number of treatments in which this occurred is indicated in brackets): *A. smithii* (5), *A.*

subsecundum (4), *A. trachycaulum* (4), *F. hallii* (4) and *S. curtiseta* (0) and in 1997, this had increased to *A. smithii* (8), *A. subsecundum* (6), *A. trachycaulum* (8), *F. hallii* (6) and *S. curtiseta* (4). Therefore, the density of each of the six grass species is becoming more variable within each treatment where it was seeded. Within the replicates of the eight treatments, often a grass species is increasing in some plots and simultaneously decreasing in other plots.

Grass species that were common to fewer treatments allowed for less comparison across the entire research site as a whole. *Stipa viridula* was seeded in four treatments. In 1997, the density of this species within the treatments is less variable than in 1996, and therefore, the species is distributed more evenly within the treatment replicates for all four treatments. *Koeleria macrantha* was seeded in three treatments and its density is also becoming less variable in 1997. *Poa palustris* is more variable in 1997 and *Bromus ciliatus* appears unchanged. P-values for these species and the remaining grass species are found in Tables 3.8 (1996) and 3.9 (1997).

Most forbs were generally not seeded in more than two treatments, making a comparison for the entire research site more ambiguous. However, *Achillea millefolium* was seeded in four treatments and in both years, the density of this species within each treatment has changed within two treatments and has not reached an equilibrium. *Oenthera biennis* was also seeded in four treatments and in 1996 it was found in three of the four treatments, but in 1997, it was not found in any of the four treatments, indicating that it could not survive possibly because of competition from other species or environmental conditions. P-values for these species and the remaining forb species are found in Tables 3.8 (1996) and 3.9 (1997).

3.4.8 Density of Individual Species

The density of some seeded species is changing significantly in relation to the total quantity of seeded plant species. The proportion of *Agropyron subsecundum* was statistically significantly different in every treatment where it was seeded. This species was identified less frequently in the permanent quadrats in 1997, possibly due to delayed seed head formation which clearly distinguishes it from *A. trachycaulum*. During late July 1996, the majority of the plants of this species had seed heads with awns which are the main distinguishing feature of *A. subsecundum*. In the vegetative

stage, it is difficult to discern from *A. trachycaulum* and therefore, the quantity of this species may not be accurate.

Other species that were statistically significantly different in 50 percent or greater of the treatments in which they were seeded include *Bromus anomalus, A. smithii, Achillea millefolium, A. trachycaulum* and *Stipa viridula. Koeleria macrantha,* and *Festuca hallii* were statistically significant in fewer than 50 percent of the treatments. The change in proportion within the seeded plant community is not consistent across all treatments. Results of this analysis are presented in Table 3.10.

3.4.9 Research Results Compared to Previous Research

Species diversity is consistent with typically three or four seeded species present within most permanent quadrats and does not vary even though the soils are quite heterogeneous throughout the research site. Therefore, Levin's (1974) premise that an increase in species richness is due to patchiness may not be true for these seeded species as the same species generally did very well or did not survive at all throughout all the treatment replicates. However, Levin's (1974) theory may be more applicable to largely undisturbed ecosystems.

The density of the most successful seeded species is quite variable amongst the treatments and the variability in density increased in 1997. Wilson's (1992) theory that the initial conditions of the site can cause large effects on the plant community development may be useful in explaining why the density of some of the plant species is becoming more variable. If a site is conducive to seed set and the seeds fall next to the parent plant, the density of that species will increase. Rhizomes will also increase the density of the rhizomatous grasses and forbs and initial favorable site conditions may make vegetative reproduction more likely.

The density of some seeded species may be increasing with the availability of resources. While the resources at the site may have made survival impossible for many of the seeded species, those that were able to acquire and use the available nutrients efficiently may be increasing in density but at different rates depending on the nutrient status. This relates to Tilman's (1982) theory that the competition for inorganic nutrients influences the community's structure. Tilman (1982) also believes that diversity will decrease on nutrient rich soils, but although the soils at the research site are quite variable (Appendix B) the seeded species diversity is very low. The

variability in the soils indicates the soil nutrients are not evenly distributed throughout the research site but the diversity of seeded plant species throughout the area is constant with the same three or four seeded species appearing in most permanent quadrats. However, the density of these species is changing which may be the formation of spatial patterns over a longer term.

Pickett et al.'s (1987) theory is difficult to incorporate into the plant community at the research site since the entire site was an open site and available for other species and the seeded species to occupy the site. Given that there were no established species on the site to provide competition, this theory may not be applicable to this research.

3.5 Conclusion

The diversity of plant species in the three to four year old plant community did not increase with a greater number of species in the seed mix. Mixes with twice as many species did not have twice the diversity compared to seed mixes containing half as many species.

The relative density or proportion of many species in the seed mix is usually reflected within the plant community. However, altering the seeding rate of some species, particularly forbs, did not alter their density in the plant community: individual plant densities are consistent relative to the same species in other treatments, regardless of the treatment.

There is statistically significant variation in plant species densities within a treatment area and the variation may increase within one growing season, indicating the treatment areas are becoming more heterogeneous and plant assembly processes are occurring. Among treatments, many grass species exhibit varying densities, possibly due to microsite conditions.

The density of some plant species is also changing significantly in relation to the total quantity of seeded plant species within each treatment plot, indicating the proportions of some species are increasing relative to the density of the entire plant community. Some species are consistently more prevalent within the plant permanent quadrats and therefore, within the plant community.

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Table 3.1 Seeding Density in Pure Live Seeds (PLS) m^{-2} and the Density of Seeded Plant Species by Treatment Totals at the Research Site in 1996 and 1997

Treatment/Species	1			6		
		Plant Density m^{-2}			Plant Density m^{-2}	
	PLS/$1m^{2**}$	1996	1997	PLS/$1m^{2**}$	1996	1997
Agropyron smithii	6.3	42	29	4.6	22	29
*Agropyron subsecundum****	14.7	24	7	10.7	30	3
*Agropyron trachycaulum****		43	37		20	60
Bromus anomalus	57.9	50	113	73.2	66	83
Festuca hallii	18.7	8	14	29.0	7	2
Stipa curtiseta	51.8	2	7	37.9	0	0

Treatment/Species	2			7		
		Plant Density m^{-2}			Plant Density m^{-2}	
	PLS/$1m^{2**}$	1996	1997	PLS/$1m^{2**}$	1996	1997
Agropyron smithii	4.3	21	31	2.7	7	20
*Agropyron subsecundum****	19.8	39	7	15.7	26	2
*Agropyron trachycaulum****		61	131		37	119
Bromus anomalus	42.2	55	148	58.1	96	150
Festuca hallii	13.8	4	4	24.0	20	17
Stipa curtiseta	37.9	6	8	23.7	0	3
Bouteloua gracilis	0.0	0	0	0.0	0	0
Bromus cilatus	3.0	2	1	1.5	9	5
Koeleria macrantha	16.1	11	4	24.1	6	13
Poa palustris	25.3	106	146	36.7	133	140
Stipa comata	12.8	0	0	6.3	0	0
Stipa viridula	5.1	12	4	7.6	11	5

Table 3.1 Seeding Density in Pure Live Seeds (PLS) m^{-2} and the Density of Seeded Plant Species by Treatment Totals at the Research Site in 1996 and 1997 (con't)

Treatment/Species	3			8		
		Plant Density m^{-2}			Plant Density m^{-2}	
	PLS/$1m^{2**}$	1996	1997	PLS/$1m^{2**}$	1996	1997
Agropyron smithii	4.4	17	22	2.8	18	43
*Agropyron subsecundum****	10.8	22	17	6.7	12	5
*Agropyron trachycaulum****		34	105		21	34
Bromus anomalus	42.2	65	217	57.9	59	217
Festuca hallii	13.8	10	65	23.9	20	16
Stipa curtiseta	38.1	0	3	23.7	4	1
Achillea millefolium	1.6	58	239	0.6	50	81
Erigeron glabellus	0.0	0	0	0.0	0	0
Anemone multifida	0.0	0	0	0.0	0	0
Monarda fistulosa	0.4	0	1	0.2	0	1
Penstemon procerus	2.8	26	30	4.0	36	24
Rumex occidentalis	1.5	1	67	1.1	0	5
Oenothera biennis	0.3	2	0	0.3	1	0

Table 3.1 Seeding Density in Pure Live Seeds (PLS) m^{-2} and the Density of Seeded Plant Species by Treatment Totals at the Research Site in 1996 and 1997 (con't)

Treatment/Species	4			9		
		Plant Density m^{-2}			Plant Density m^{-2}	
	PLS/$1m^{2**}$	1996	1997	PLS/$1m^{2**}$	1996	1997
Agropyron smithii	4.3	41	51	2.7	13	20
*Agropyron subsecundum****	10.8	29	19	6.8	21	33
*Agropyron trachycaulum****		36	110		30	58
Bromus anomalus	42.2	69	114	58.1	74	195
Festuca hallii	13.8	1	5	24.0	4	51
Stipa curtiseta	37.9	1	2	23.7	0	14
Achillea millefolium	1.1	29	95	0.6	46	141
Erigeron glabellus	0.0	0	0	0.0	0	0
Anemone multifida	0.0	0	0	0.0	0	0
Monarda fistulosa	0.4	0	0	0.2	1	0
Oenothera biennis	0.3	1	0	0.3	0	0
Oxytropis deflexa	6.5	9	3	3.2	2	0
Oxytropis splendens	1.7	3	0	2.6	0	0

Treatment/Species	5		
		Plant Density m^{-2}	
	PLS/$1m^{2**}$	1996	1997
Agropyron riparian	28.5	65	55
Agropyron smithii	8.8	34	34
Agropyron trachycaulum	19.4	73	147
Festuca hallii	25.0	34	35
Festuca ovina	31.8	15	14
Festuca rubra	19.4	94	374
Koeleria macrantha	16.1	5	1
Poa alpina	15.8	19	34
Stipa viridula	4.5	3	1

Table 3.1 Seeding Density in Pure Live Seeds (PLS) m^{-2} and the Density of Seeded Plant Species by Treatment Totals at the Research Site in 1996 and 1997 (con't)

Treatment/Species	10		
		Plant Density m^{-2}	
	PLS/1m^{2*}	1996	1997
Agropyron dasystachyum	18.6	67	62
Agropyron intermedium	4.1	32	6
Agropyron smithii	13.1	63	98
*Agropyron subsecundum***	5.6	9	2
*Agropyron trachycaulum****		60	119
Stipa viridula	11.5	16	16
Medicago sativa	2.4	3	0

*Treatment totals = 10 x 0.1 m^2 quadrat or 1 m^2 area.
**based on field germination rates (Bush 1998).
No germination rates for *Monarda*, therefore entered 2 percent; Germination rate for *Penstemon procerus* is 0 percent, therefore entered 10 percent (Bush 1998).
***Agropyron subsecundum* and *Agropyron trachycaulum* were combined in seed mix but counted as separate species in the plant community.

Table 3.2 Chi Square Analysis of Seeded Species Diversity Among Individual Quadrats at the Research Site in 1996 and 1997

Treatment	p-value 1996	p-value 1997	Treatment	p-value 1996	p-value 1997
A1:1	0.45	0.96	A1:6	0.13	NA
A2:1	0.29	0.59	A2:6	0.96	0.97
B3:1	0.85	0.98	B3:6	0.74	0.91
C4:1	0.36	0.74	C4:6	0.37	0.47
C5:1	0.99	0.96	C5:6	0.88	1.00
A1:2	0.98	0.56	A1:7	0.90	0.59
A2:2	0.89	0.60	A2:7	0.95	0.67
B3:2	0.97	0.93	B3:7	0.98	0.94
C4:2	1.00	0.98	C4:7	0.99	0.97
C5:2	0.94	0.74	C5:7	1.00	0.93
A1:3	0.69	0.90	A1:8	0.53	0.86
A2:3	0.94	0.99	A2:8	0.06	0.55
B3:3	0.95	0.99	B3:8	0.91	0.90
C4:3	0.12	0.98	C4:8	0.21	0.73
C5:3	0.85	0.60	C5:8	0.85	0.73
A1:4	0.81	0.73	A1:9	0.90	0.78
A2:4	0.90	0.88	A2:9	0.94	0.96
B3:4	0.88	0.64	B3:9	0.77	0.93
C4:4	0.36	0.66	C4:9	0.94	0.85
C5:4	0.53	0.82	C5:9	0.64	0.35
A1:5	0.96	0.99	A1:10	0.35	0.56
A2:5	1.00	0.74	A2:10	0.96	0.98
B3:5	0.83	0.73	B3:10	0.85	0.99
C4:5	0.82	0.65	C4:10	0.21	0.83
C5:5	0.93	0.99	C5:10	0.31	0.97

NA = Not available; only one seeded plant species growing in 10 quadrats.
A p-value less than 0.05 is required to reject the null hypothesis.

Table 3.3 Chi Square Analysis of Seeded Species Diversity Among Treatment Replicates at the Research Site in 1996 and 1997

	p-value	
Treatment	1996	1997
1	0.96	0.99
2	0.95	0.89
3	0.95	0.93
4	0.88	0.99
5	0.95	0.99
6	0.82	0.39
7	0.99	0.97
8	0.98	0.95
9	1.00	0.98
10	0.99	0.97

A p-value less than 0.05 is required to reject the null hypothesis.

Table 3.4 Ranking Analysis of Seed Quantity versus Plant Density Within Plots at the Research Site in 1996 and 1997

Treatment	1996		Treatment	1996	
	Spearman's P-value	Correlation Coefficient		Spearman's P-value	Correlation coefficient
A1:1	0.86	0.11	A1:6	0.72	0.22
A2:1	0.62	0.30	A2:6	0.81	0.15
B3:1	0.62	0.30	B3:6	0.87	0.10
C4:1	0.51	0.40	C4:6	0.49	0.41
C5:1	0.22	0.67	C5:6	0.81	0.15
A1:2	0.20	0.44	A1:7	0.14	0.50
A2:2	0.18	0.46	A2:7	0.06	0.61
B3:2	0.01	0.79	B3:7	0.05	0.64
C4:2	0.44	0.28	C4:7	0.12	0.52
C5:2	0.08	0.59	C5:7	0.27	0.39
A1:3	0.12	0.53	A1:8	0.24	0.41
A2:3	0.08	0.58	A2:8	0.01	0.83
B3:3	0.11	0.53	B3:8	0.11	0.54
C4:3	0.52	0.23	C4:8	0.45	0.26
C5:3	0.69	0.14	C5:8	0.62	0.18
A1:4	0.31	0.36	A1:9	0.07	0.60
A2:4	0.15	0.49	A2:9	0.20	0.45
B3:4	0.69	0.14	B3:9	0.39	0.30
C4:4	0.34	0.34	C4:9	0.69	0.14
C5:4	0.37	0.32	C5:9	0.37	0.32
A1:5	0.73	0.14	A1:10	0.07	0.77
A2:5	0.22	0.45	A2:10	0.04	0.83
B3:5	0.14	0.54	B3:10	0.29	0.52
C4:5	0.34	0.36	C4:10	0.05	0.81
C5:5	0.55	0.25	C5:10	0.54	0.32

Table 3.4 Ranking Analysis of Seed Quantity versus Plant Density Within Plots at the Research Site in 1996 and 1997 (con't)

Treatment	1997 Spearman's P-value	1997 Correlation Coefficient	Treatment	1997 Spearman's P-value	1997 Correlation Coefficient
A1:1	0.74	0.21	A1:6	0.18	0.71
A2:1	0.55	0.36	A2:6	0.18	0.71
B3:1	0.62	0.30	B3:6	0.81	0.15
C4:1	0.81	0.15	C4:6	0.87	0.10
C5:1	0.55	0.36	C5:6	0.81	0.15
A1:2	0.14	0.51	A1:7	0.15	0.49
A2:2	0.07	0.60	A2:7	0.02	0.72
B3:2	0.05	0.64	B3:7	0.02	0.72
C4:2	0.16	0.49	C4:7	0.31	0.36
C5:2	0.11	0.54	C5:7	0.21	0.43
A1:3	0.23	0.42	A1:8	0.31	0.36
A2:3	0.01	0.76	A2:8	0.66	0.16
B3:3	0.77	0.11	B3:8	0.12	0.52
C4:3	0.37	0.32	C4:8	0.26	0.39
C5:3	0.87	0.06	C5:8	0.38	0.31
A1:4	0.13	0.51	A1:9	0.04	0.65
A2:4	0.21	0.44	A2:9	0.12	0.52
B3:4	0.58	0.20	B3:9	0.21	0.43
C4:4	0.48	0.25	C4:9	0.61	0.18
C5:4	0.48	0.25	C5:9	0.23	0.42
A1:5	1.00	1.00	A1:10	0.00	0.97
A2:5	0.20	0.40	A2:10	0.21	0.60
B3:5	0.20	0.47	B3:10	0.35	0.46
C4:5	0.46	0.28	C4:10	0.17	0.64
C5:5	0.40	0.32	C5:10	0.13	0.70

A p-value of less than 0.05 is required to reject the null hypothesis.

Table 3.5 Ranking Analysis of Statistically Significant Treatments (from Table 3.4) versus Remaining Treatments at the Research Site in 1996 and 1997

Treatment	vs.	Treatment	1996		1997	
			Spearman's P-value	Correlation Coefficient	Spearman's P-value	Correlation Coefficient
2		1	0.04	0.90	0.04	0.90
2		3	0.10	0.80	0.19	0.70
2		4	0.05	0.87	0.10	0.80
2		6	0.10	0.80	0.04	0.90
2		7	0.29	0.60	0.04	0.90
2		8	0.29	0.60	0.10	0.80
2		9	0.10	0.80	0.19	0.70
7		1	0.10	0.80	0.00	1.00
7		3	0.04	0.90	0.04	0.90
7		4	0.09	0.82	0.04	0.90
7		6	0.04	0.90	0.00	1.00
7		8	0.00	1.00	0.04	0.90
7		9	0.04	0.90	0.04	0.90

The six core grass species were used for this comparison.
A p-value less than 0.05 is required to reject the null hypothesis.

Table 3.6 Chi Square Analysis of the Density of All Seeded Species Within Quadrats at the Research Site in 1996 and 1997

Treatment	p-value 1996	p-value 1997	Treatment	p-value 1996	p-value 1997
A1:1	0.04	0.01	A1:6	0.01	0.44
A2:1	0.03	0.00	A2:6	0.79	0.73
B3:1	0.04	0.06	B3:6	0.72	0.17
C4:1	0.08	0.01	C4:6	0.04	0.00
C5:1	0.07	0.00	C5:6	0.72	0.02
A1:2	0.00	0.21	A1:7	0.00	0.00
A2:2	0.22	0.00	A2:7	0.31	0.00
B3:2	0.44	0.00	B3:7	0.00	0.00
C4:2	0.30	0.00	C4:7	0.00	0.01
C5:2	0.21	0.00	C5:7	0.63	0.00
A1:3	0.00	0.00	A1:8	0.00	0.01
A2:3	0.00	0.00	A2:8	0.00	0.01
B3:3	0.13	0.00	B3:8	0.49	0.00
C4:3	0.00	0.00	C4:8	0.00	0.00
C5:3	0.19	0.00	C5:8	0.67	0.03
A1:4	0.00	0.15	A1:9	0.00	0.00
A2:4	0.02	0.00	A2:9	0.22	0.00
B3:4	0.03	0.00	B3:9	0.01	0.23
C4:4	0.01	0.00	C4:9	0.03	0.00
C5:4	0.05	0.00	C5:9	0.02	0.00
A1:5	0.58	0.24	A1:10	0.00	0.00
A2:5	0.01	0.00	A2:10	0.09	0.16
B3:5	0.10	0.01	B3:10	0.82	0.08
C4:5	0.02	0.00	C4:10	0.00	0.00
C5:5	0.19	0.00	C5:10	0.00	0.00

A p-value less than 0.05 is required to reject the null hypothesis.

Table 3.7 Chi Square Analysis of Seeded Species Evenness Within Each Plot at the Research Site in 1996 and 1997

	p-value			p-value	
Treatment	1996	1997	Treatment	1996	1997
A1:1	0.00	0.00	A1:6	0.07	0.41
A2:1	0.00	0.00	A2:6	0.00	0.00
B3:1	0.00	0.00	B3:6	0.00	0.02
C4:1	0.07	0.00	C4:6	0.04	0.00
C5:1	0.00	0.00	C5:6	0.00	0.00
A1:2	0.00	0.00	A1:7	0.00	0.00
A2:2	0.00	0.00	A2:7	0.00	0.00
B3:2	0.00	0.00	B3:7	0.00	0.00
C4:2	0.00	0.00	C4:7	0.00	0.00
C5:2	0.00	0.00	C5:7	0.00	0.00
A1:3	0.00	0.00	A1:8	0.00	0.00
A2:3	0.00	0.00	A2:8	0.00	0.00
B3:3	0.00	0.00	B3:8	0.00	0.00
C4:3	0.00	0.00	C4:8	0.00	0.00
C5:3	0.00	0.00	C5:8	0.00	0.00
A1:4	0.00	0.00	A1:9	0.00	0.00
A2:4	0.00	0.00	A2:9	0.00	0.00
B3:4	0.00	0.00	B3:9	0.00	0.00
C4:4	0.00	0.00	C4:9	0.00	0.00
C5:4	0.00	0.00	C5:9	0.00	0.00
A1:5	0.00	0.00	A1:10	0.00	0.00
A2:5	0.00	0.00	A2:10	0.00	0.00
B3:5	0.00	0.00	B3:10	0.00	0.00
C4:5	0.00	0.00	C4:10	0.00	0.00
C5:5	0.00	0.00	C5:10	0.00	0.00

A p-value less than 0.05 is required to reject the null hypothesis.

Table 3.8 Chi Square Analysis of Species Density Among Treatment Replicates at the Research Site in 1996

	Trt 1	Trt 2	Trt 3	Trt 4	Trt 5	Trt 6	Trt 7	Trt 8	Trt 9	Trt 10	Total	Mean
A. smithii	0.00	0.00	0.23	0.05	0.00	0.02	0.02	0.54	0.06	0.02	**0.94**	0.09
A. subsecundum	0.20	0.00	0.01	0.03	0.04	0.00	0.58	0.18	0.41	0.44	**1.88**	0.19
A. trachycaulum	0.00	0.17	0.38	0.00		0.05	0.05	0.89	0.23	0.09	**1.85**	0.21
B. anomalus	0.00	0.00	0.00	0.00		0.00	0.00	0.01	0.01		**0.02**	0.00
F. halli	0.14	0.48	0.00	0.41	0.14	0.01	0.00	0.00	0.48		**1.66**	0.18
S. curtiseta	0.09	0.23	**0**	0.41		**0**	**0**	0.07	**0**		**0.80**	0.10
B. cilatus		0.56					0.00				**0.56**	0.28
K. macrantha		0.41			0.02		0.00				**0.43**	0.14
P. palustris		0.25					0.00				**0.25**	0.13
S. comata		**0**					**0**				**0.00**	0.00
S. viridula		0.02			0.25		0.00			0.41	**0.68**	0.17
A. millefolium			0.45	0.00				0.00	0.00		**0.45**	0.11
M. fistulose			**0**	**0**				**0**	0.41		**0.41**	0.10
P. procerus			0.00					0.01			**0.01**	0.00
R. occidentalis			0.41					**0**			**0.41**	0.20
O. biennis			0.56	0.41				0.41	**0**		**1.37**	0.34
O. deflexa				0.00					0.56		**0.56**	0.28
O. splendens				0.02					**0**		**0.02**	0.01
A. riparian					0.18						**0.18**	0.18
F. ovina					0.02						**0.02**	0.02
F. rubra					0.05						**0.05**	0.05
P. alpina					0.04						**0.04**	0.04
A. dasystachyum										0.08	**0.08**	0.08
A. intermedium										0.00	**0.00**	0.00
M. sativa										0.25	**0.25**	0.25
Total	**0.43**	**2.10**	**2.03**	**1.32**	**0.74**	**0.09**	**0.66**	**2.10**	**2.16**	**1.28**	**12.90**	**3.17**
Mean	0.07	0.19	0.18	0.12	0.06	0.01	0.06	0.19	0.20	0.18	0.52	0.13

Bold zeros indicate the plant species was not found within the permanent quadrats.
A p-value less than 0.05 is required to reject the null hypothesis.

Table 3.9 Chi Square Analysis of Species Density Among Treatment Replicates at the Research Site in 1997

	Trt 1	Trt 2	Trt 3	Trt 4	Trt 5	Trt 6	Trt 7	Trt 8	Trt 9	Trt 10	Total	Mean
A. smithii	0.00	0.02	0.01	0.00	0.11	0.01	0.00	0.00	0.02	0.00	**0.17**	0.02
A. subsecundum	0.00	0.00	0.00	0.00	0.55	0.02	0.56	0.09	0.00	0.09	**1.31**	0.13
A. trachycaulum	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	**0.00**	0.00
B. anomalus	0.00	0.00	0.00	0.00		0.00	0.02	0.00	0.00		**0.02**	0.00
F. halli	0.00	0.48	0.00	0.02	0.10	0.09	0.00	0.00	0.00		**0.69**	0.08
S. curtiseta	0.02	0.01	0.02	0.09		**0**	0.25	0.41	0.00		**0.80**	0.10
B. ciatus		0.41					0.00				**0.41**	0.20
K. macrantha		0.48			0.41		0.00				**0.88**	0.29
P. palustris		0.00					0.00				**0.00**	0.00
S. comata		**0**					**0**				**0.00**	0.00
S. viridula		0.07			0.41		0.41			0.13	**1.02**	0.25
A. millefolium			0.00	0.00				0.00	0.21		**0.21**	0.05
M. fistulosa			0.41	**0**				0.41	**0**		**0.81**	0.20
P. procerus			0.00					0.00			**0.00**	0.00
R. occidentalis			0.00					0.02			**0.02**	0.01
O. biennis			**0**	**0**				**0**	**0**		**0.00**	0.00
O. deflexa				0.02					**0**		**0.02**	0.01
O. splendens				**0**					**0**		**0.00**	0.00
A. riparian					0.13						**0.13**	0.13
F. ovina					0.00						**0.00**	0.00
F. rubra					0.00						**0.00**	0.00
P. alpina					0.00						**0.00**	0.00
A. dasystachyum										0.01	**0.01**	0.01
A. intermedium										0.23	**0.23**	0.23
M. sativa										**0**	**0.00**	0.00
Total	**0.02**	**1.47**	**0.43**	**0.13**	**1.71**	**0.12**	**1.24**	**0.92**	**0.22**	**0.46**	**6.71**	**1.72**
Mean	0.00	0.13	0.04	0.01	0.19	0.02	0.11	0.08	0.02	0.07	**0.27**	0.07

Bold, single zeros indicate the plant species was not found within the permanent quadrats.
A p-value less than 0.05 is required to reject the null hypothesis.

Table 3.10 Proportion Analysis of the Density of Individual Species at the Research Site During 1996 and 1997

Treatment 1	# of Std. Errors	Treatment 6	# of Std. Errors
A. smithii	2.7	*A. smithii*	0.3
A. subsecundum	3.8	*A. subsecundum*	5.6
A. trachycaulum	1.8	*A. trachycaulum*	4.2
B. anomalus	4.9	*B. anomalus*	0.2
F. hallii	0.8	*F. hallii*	2.0
S. curtiseta	1.4	*S. curtiseta*	0.0
Treatment 2		**Treatment 7**	
A. smithii	0.1	*A. smithii*	1.7
A. subsecundum	6.5	*A. subsecundum*	5.5
A. trachycaulum	2.5	*A. trachycaulum*	5.2
B. anomalus	4.2	*B. anomalus*	1.2
F. hallii	0.6	*F. hallii*	1.5
S. curtiseta	0.3	*S. curtiseta*	1.5
B. ciliatus	1.0	*B. ciliatus*	1.7
K. macrantha	2.7	*K. macrantha*	0.9
P. palustris	1.0	*P. palustris*	2.7
S. comata	0.0	*S. comata*	0.0
S. viridula	2.9	*S. viridula*	2.2
Treatment 3		**Treatment 8**	
A. smithii	3.0	*A. smithii*	0.8
A. subsecundum	5.0	*A. subsecundum*	3.2
A. trachycaulum	0.3	*A. trachycaulum*	0.7
B. anomalus	0.1	*B. anomalus*	5.8
F. hallii	2.1	*F. hallii*	2.8
S. curtiseta	1.0	*S. curtiseta*	2.2
A. millefolium	1.9	*A. millefolium*	1.1
M. fistulosa	0.6	*M. fistulosa*	0.7
P. procerus	4.2	*P. procerus*	4.5
R. occidentalis	4.4	*R. occidentalis*	1.6
O. biennis	2.6	*O. biennis*	1.4

Table 3.10 Proportion Analysis of the Density of Individual Species at the Research Site During 1996 and 1997 (con't)

Treatment 4	# of Std. Errors	Treatment 9	# of Std. Errors
A. smithii	2.0	*A. smithii*	1.6
A. subsecundum	3.8	*A. subsecundum*	2.0
A. trachycaulum	3.1	*A. trachycaulum*	1.6
B. anomalus	0.8	*B. anomalus*	0.2
F. hallii	1.0	*F. hallii*	3.5
S. curtiseta	0.1	*S. curtiseta*	2.3
A. millefolium	3.1	*A. millefolium*	0.9
M. fistulosa	0.0	*M. fistulosa*	1.6
O. biennis	1.4	*O. biennis*	0.0
O. deflexa	2.9	*O. deflexa*	2.3
O. splendens	0.0	*O. splendens*	0.0
Treatment 5		**Treatment 10**	
A. riparian	5.2	*A. dasystachyum*	1.8
A. smithii	3.1	*A. intermedium*	5.0
A. trachycaulum	0.1	*A. smithii*	1.8
F. hallii	3.0	*A. subsecundum*	2.5
F. ovina	2.2	*A. trachycaulum*	3.8
F. rubra	8.0	*S. viridula*	0.6
K. macrantha	2.6	*M. sativa*	1.9
P. alpina	0.5		
S. viridula	1.8		

The number of standard errors must be less than 2.0 to reject the null hypothesis.

CHAPTER FOUR
SOIL SALINITY AND THE DISTRIBUTION OF PLANT SPECIES

4.1 Introduction

Plant germination, growth and survivability is affected by soil chemical parameters, particularly the presence of sodium and soluble salts. In addition to electrical conductivity (EC) and exchangeable sodium percentage (ESP) as indicators of soil salinity, if soluble salts are present in sufficient quantities to affect plant growth, then the soil is considered saline (Marschner 1986). In species that are not adapted to saline soils, low concentrations of sodium chloride, sodium sulfate, calcium chloride, magnesium chloride and magnesium sulfate can inhibit growth due to ion toxicity. Sodic and saline-sodic soils are usually limiting due to the unavailability of water and nutrients and toxicity of chlorine, sodium and boron (Marschner 1986).

During germination, the effect of salinity is at its greatest, due to the surface layers of soil accumulating salts as evaporation and capillary rise occurs (Hayward and Bernstein 1958) and can result in bare patches of soil. The first increments of salinity tend to retard germination and additional increments tend to reduce progressively the final percent germination (Hayward and Bernstein 1958). Moreover, the correlation of salt tolerance in germination to salt tolerance at later growth stages is poor.

McGinnies et al. (1976), Bowman et al. (1985) and Kreeb et al. (1995) indicated that species diversity declines on most salt-affected soils above a threshold level. With increasing environmental stress, species diversity is reduced and limited to the species that have tolerance for the specific conditions (Grime 1973). Plant species are generally confined to areas where the soil conditions are appropriate for their nutritional and hydrologic requirements and within their tolerance for toxic ions (McGinnies et al. 1976; Bowman et al. 1985; Kreeb et al. 1995). With an increasing variety of soil conditions, the number of species increased accordingly in all three field studies. Densities of species with limited ability to invade surrounding, heterogeneous patches were lower in the heterogeneous patches. The most salt-tolerant species were not found outside of the highly saline patches. Species located in less saline and/or sodic areas seemed to be found in patches with a narrow range of chemical and physical parameters.

Thus, a relationship between plant species diversity and the salt content soils appears to be present. Generally, plant growth becomes affected by the presence of sodium and/or salts when SAR and EC levels exceed critical values of 15 and 4 dS m^{-1}, respectively (Marschner 1986). However, these values are not exact indicators of a species salt tolerance, as variance for salt-tolerance may be as great as the pH variance tolerated by the *Plantago* species researched by Van Der Aart (1985).

Low plant density is associated with low population growth rates, produced by a deficiency in one or more essential resources (Huston 1979). This hypothesis can explain the findings in each of the three field studies, as density of vegetation located within the high SAR and EC microsites was generally lower relative to surrounding areas with lower SAR and EC values (McGinnies et al. 1976; Bowman et al. 1985; Kreeb et al. 1995).

Huston (1979) examined the relationship between density and diversity. Within a low density community, plant species could potentially mirror the heterogeneity in soils, while within a high density community, species could enter into less preferred soils due to crowding and mask the subtle soil differences. Bowman et al. (1985) analysed the same site for three years and found the species composition within the permanent quadrats did vary, but total cover was less variable. Therefore, species may be entering into areas that are different from their preferred soils, regardless of the change in total density.

The vegetation patterns discovered in the Colorado/Wyoming studies indicate that saltgrass can be found in microsites where SAR and EC is high (McGinnies et al. 1976; Bowman et al. 1985). The assembly rules that govern the formation of patterns are important in understanding how the communities studied by McGinnies et al. (1976) Bowman et al. (1985), and Kreeb et al. (1995) were formed, according to Weiher and Keddy (1995). Why the species composition variability within the permanent quadrats exists when the soils are heterogeneous is unknown (Bowman et al. 1985). Research by McGinnies et al. (1976) and Kreeb et al. (1995) indicated that the salt-tolerant species mirrored the changes in soil conditions. Alternatively, Van Der Aart (1985) found two *Plantago* species were able to inhabit a wide variety of habitats with varying soil chemical properties.

4.2 Research Objectives and Hypothesis

4.2.1 Research Objectives

The general research objective is to determine if native plant community assembly processes can be predicted. Specifically, the objective is to determine if native plant species composition and/or density is affected by soil salinity.

Research, published in English in this subject area, is limited to the native plants of Colorado/Wyoming and New South Wales areas for plant species native to those areas. Both of these research groups have examined native plant vegetation patterns on saline and non-saline soils and found evidence of vegetative patterns that coincide with soil salinity (McGinnies et al. 1976; Bowman et al. 1985; Kreeb et al. 1995). However, more research is required as plant species native to Alberta are being used in land reclamation with the intent of forming healthy, sustainable plant communities across a variety of soil salinity conditions. Whether these commonly used native grass and forb species can adapt and thrive in a range of soil salinity conditions is unknown.

4.2.2 Hypothesis

Plant community development is driven by microsite soil conditions that alter the establishment and persistence of individual plant species.

4.3 Experimental Design and Methods

4.3.1 Site Description

The research site is located within the Aspen Parkland Ecoregion at the Parkland Agricultural Research Initiative (PARI) Conservation Farm, close to Mundare, Alberta, 100 km east of Edmonton (NE and SE quarters of Sec 9, T53, R16, W of the 4th meridian). There are five blocks within the research site: A1, A2, B3, C4 and C5. (Appendix A: Figures A.1, A.2 and A.3). Clones of aspen are dominant and interspersed with grasslands throughout this region (Moss 1932).

The mean rainfall is 318.4 mm annually with the greatest rainfall occurring during July (83.2 mm) and June (73.0 mm) (Environment Canada 1993). During the winter months, 83.8 cm of snow falls on average (Environment Canada 1993).

The mean temperatures rise above 0 °C in April (3.4 °C) and remain above freezing until October (4.2 °C) (Environment Canada 1993). The highest mean temperature occurs during July at 16.2 °C followed by August at 15.2 °C and June at 14.4 °C. June, July and August are the only months when there are no degree days below 0 °C. The annual mean is 1.4 °C (Environment Canada 1993).

Black Chernozemic soils, formed under the grassland vegetation are typical, with Dark Gray Chernozems occupying areas where the aspen forests have been established for long periods, causing eluviation (Strong and Leggat 1981). These soils are typically moderately well drained.

Chernozemic, Solonetzic and Gleysolic soils groups are mixed within plots (Walker 1992). Forty percent of the seeded area contains 70 percent Solonetzic soils at blocks C:4 and C:5. The Solonetzic soils occur randomly on mid-slope to hilltop positions where salts are near the surface. At C4 and C5, 30 to 40 percent of the area is a Black Solodized Solonetzic, 20 to 30 percent Solonetzic Black Chernozemic and 15 to 20 percent Humic Gleysolic soils. Gleysolic soils are found in the center depressional area in C:4 and C:5. Additional information on the soils at the research site is in Appendix B.

4.3.1.1 Site History

The areas for the research site were randomly chosen within the PARI Farm. Five blocks were randomly selected from a possible twelve blocks. Each block was formerly a tame pasture composed mainly of *Bromus inermis* and *Poa pratensis* that was sprayed with glyphosate at a rate of 3.7 L. per hectare on July 13, 1993 (Kupchenko 1998). A heavy breaking plow was used to break the site on August 16, 1993 and a lighter disk was utilized later in August and November and in the spring of the following year. Blocks A1, A2 and B3 were disked and cultivated once more before seeding, while C4 and C5 were cultivated and harrow-packed before seeding (Bush 1998). Species native to the Aspen Parkland were seeded in spring 1994, using six species seed mixes in ten (9.2 x 18.3 m) plots in each of five blocks. Within each block, each treatment was randomly chosen. Four of the six seed mixes have species combinations that were replicated twice, but the density of each species was altered to produce a unique treatment. The remaining two mixes were applied at only one

seeding rate. Hence, there are ten treatments, each replicated five times for a total of 50 plots. Refer to Appendix B for seed mixes and seeding rates.

4.3.2 Soil Sampling and Analysis

4.3.2.1 Electrical Conductivity

In early June 1997, each plot was assessed for soil characteristics with a Geonics EM38 Ground Conductivity Meter to measure soil conductivity. For each plot, a preliminary analysis was conducted, which consisted of taking measurements in rows 2 m apart at 1 m intervals along each 18.3 m row. Where the EM38 data were quite variable, further readings were taken between the initial rows, so the entire plot had a data point at each 1 m^2 interval. Therefore, six 20 m rows of data were taken for the preliminary analysis compared to 11 rows for a full 1 m^2 analysis of the plot. Horizontal and vertical readings were taken at each data point to provide information on the soil profile. Horizontal measurements indicate the apparent conductivity at the soil surface while the vertical measurements record the apparent conductivity to a 1.5 m depth with a maximum sensitivity at 0.4 m.

The EM38 data were divided into 4 categories, with each category assigned a colour. The EM38 values are provided in brackets. White: non-saline (< 50); light gray: very weak salinity (50 to 79); dark gray: moderately saline (80 to 119); and black: saline (>120). These categories were formulated based on soil survey information obtained from Agriculture and Agri-Food Canada (Walker 1997). EM38 values less than 50 are considered non-saline regardless of soil moisture conditions, while EM38 values of approximately 80 indicates some salinity is present. EM38 values greater than 100 indicate the soil is saline. These ranges correlate loosely with the general classification for soil salinity whereby < 4 dS/m indicates non-saline or low saline conditions, 4.1 to 8 dS/m is moderately saline, 8.1 to 12 dS/m is highly saline and > 12 dS/m is strongly saline (Lilley 1982).

After the EM38 data were divided into categories, colour plot maps for the horizontal and vertical data were constructed. In determining where to conduct further research, two criteria had to be met: 1) the plots had to contain a range of non-saline areas to moderately saline areas as a basis for comparison to determine if EC was a major contributing factor for changes in species composition and/or density; 2) the

EM38 values had to be relatively consistent throughout the soil profile so that the plant species would have likely experienced the same degree of salinity from germination to maturity. The horizontal and vertical maps of each plot were then analyzed to see which plots met the criteria.

Five plots had a wide range of EM38 values, from non-saline to moderately saline, that were consistent within the soil profile. Within one of these plots, seeding problems in 1994 encompassed the low and high EM38 ranges so a comparison of plant species and their density would not be valid. A second plot was subsequently disqualified in July when second EM38 readings were taken prior to placing quadrat location flags within the plots. The plot no longer had non-saline EM38 values due to drier soil conditions which increased the EM38 readings to values greater than 50. The remaining three plots also had drier soils, but the EM38 values for the non-saline areas within these plots were less than 50. Therefore, three plots, each with a different seeding treatment, met the criteria. The EM38 data maps of the three plots are Figures 4.1, 4.2, 4.3, 4.4, 4.5 and 4.6.

4.3.3 Vegetation Sampling and Analysis

4.3.3.1 Species Assessment

The vegetation within the three plots was assessed to determine if vegetation patterns were present that denote the soil conditions. Thirty 0.1 m^2 quadrats were placed within each plot: 15 where the highest EM38 readings occurred and 15 where the lowest EM38 readings were observed. EM38 readings were taken prior to flagging the quadrat to ensure the values were less than 50 for the non-saline areas, 80 or greater for the moderately saline to saline areas. Areas with the highest horizontal and vertical EM38 values were chosen for quadrat placement within the high EC areas, while areas with the lowest EM38 values were chosen for quadrat placement in the low EC areas. Quadrats were spaced at least 30 cm apart and centered around the flag with a consistent orientation for the species composition/density measurements. Species composition and density assessments were completed in late July 1997. Plant species were identified and the individual plants counted within each quadrat to determine the density of each species. All plants were counted as separate individuals as tillered (vegetatively reproduced) plants could not be determined accurately without

digging. The total density and mean for each species are in Table 4.1 (Plot C5:6), Table 4.2 (Plot C5:4) and Table 4.3 (Plot C4:8).

4.3.4 Statistical Analyses

A Chi Square analysis was performed to determine if the number of seeded species were statistically significant between high and low EC areas within a plot and amongst the plots. The level of significance chosen on the advice of Dr. F. Yeh (1997) was 0.05. SPSS was the statistical software used. To determine the competitive influence of *Cirsium arvense* on the seeded species, a ranking test was performed using Spearman's correlation coefficient method using SPSS software.

4.3.4.1 Density of Seeded Species Between High and Low EC Areas Within a Plot

A Chi Square analysis was undertaken to determine if certain plant species were statistically significantly more prevalent within specific soil EC areas. Only seeded species were analysed since the objective of the research was to determine the species that could be suitable for reclaiming areas with varying degrees of salinity. Therefore, non-seeded species were not included in the Chi Square analysis except for *Achillea millefolium* and *Penstemon procerus* which were not seeded in all treatments but were present in all plots.

The Chi Square analysis tested the plant density of each seeded species between the high and low EC areas within the same plot. The null hypothesis states that there is no difference between the number of plants of a specific species in the high and low EC areas of the same plot. A p-value less than 0.05 would indicate that there is a difference in the plant densities that could be possibly due to variable EC conditions.

4.3.4.2 Density of Seeded Species in High and Low EC Areas Among Plots

A Chi Square analysis was performed to determine if there is a statistically significant difference in the density of a plant species in each of the high and low EC areas among the three plots. The null hypothesis states that there is no difference in a plant species density among the plots for a plant species in a low EC (or high EC)

area. Therefore, a plant species that may have a greater density in the non-saline area of one plot may also have greater densities in the low EC areas of the remaining two plots. These densities may not be statistically significantly different, indicating the plant species is found in relatively consistent densities among all low EC plot areas.

4.3.4.3 Density of *Cirsium arvense* and Seeded Species Within Plots

A ranking analysis was used to determine if the density of *Cirsium arvense* was contributing to the lower densities of the seeded species, especially in the non-saline, low EC areas. The density of *C. arvense* within each quadrat was compared to the total number of seeded species present within the quadrat to see if there was a negative correlation. The null hypothesis states that there is no difference in the relative density of the seeded species and the relative density of *Cirsium arvense* within each quadrat. Therefore, a p-value of less than 0.05 and a high, (> 0.700) negative correlation coefficient would indicate that the density of *Cirsium arvense* may be influencing the density of other seeded species.

4.4 Results and Discussion

4.4.1 Plant Species Composition

The plant species found within the sampled quadrats at plot C5:6 included all the seeded species (*Agropyron smithii, A. trachycaulum, Bromus anomalus, Festuca hallii* and *Stipa curtiseta*) except for *A. subsecundum* which was absent in both the high and low EC areas and *F. hallii* which was not found in the low EC areas. Other species commonly found within the quadrats included *Poa palustris, P. pratensis, Bromus inermis, Sonchus* spp., *Achillea millefolium, Penstemon procerus, Agrostis scabra, Potentilla norvegica, Crepis tectorum, Plantago major* (high EC), *Artemisia absynthium* (high EC), *Thlaspi arvense* (low EC) and *Cirsium arvense*.

At plot C5:4, the majority of the seeded grass species were found within the sampled quadrats except for *Agropyron subsecundum* and *Festuca hallii* which were not found in the low EC areas. The only seeded forb present was *Achillea millefolium* and it was more prevalent in the high EC areas. Common non-seeded species found within the quadrats included *Poa palustris, P. pratensis, Agrostis scabra, Cirsium arvense, Polygonum convolvulus, Artemisia frigida, Sonchus* spp., *Potentilla norvegica*

(low EC), *Bromus inermis* (low EC), *Bromus ciliatus* (high EC), *Geum* spp. (high EC), *Penstemon procerus* (high EC) and *Carex* spp. (high EC). Common names for these species are presented in Appendix B.

Within plot C4:8, the seeded grass species growing within the quadrats were all represented within the high EC areas except for *Agropyron subsecundum* and *Festuca hallii*. Of the seeded forbs, *Achillea millefolium* was the only species found in both high and low EC areas, while *Penstemon procerus and Rumex occidentalis* were found only in the high and low EC areas, respectively. The common non-seeded species included *Poa palustris* (low EC), *P. pratensis, Agrostis scabra, Potentilla norvegica* (low EC), *Taraxacum officinale, Polygonum convolvulus, Artemisia frigida, A. absynthium, Axyris amaranthoides, Cirsium arvense, Sonchus* spp., *Bromus inermis* (low EC), *Bromus ciliatus* (high EC), *Geum* spp. (high EC) and *Penstemon procerus* (high EC). Common names for these species are presented in Appendix B.

4.4.2 Density of Seeded Species Between High and Low EC Areas Within a Plot

4.4.2.1 Plot C5:6

Bromus anomalus, Stipa curtiseta and *Festuca hallii* had densities that were not statistically significantly different between the high and low EC areas. *Festuca hallii* was not present in the low EC areas and only three plants were found within the high EC quadrats. Statistically, this indicates that the three *Festuca hallii* plants could be within the quadrats simply due to chance since there are less than five plants present. A value of five is deemed to be the statistical threshold for randomness and chance (Yeh 1997). *Agropyron subsecundum* was not found in either area so it was not included in the analysis. Therefore, the seeded species that were statistically significantly different between the high and low EC areas within C5:6 were *Agropyron smithii* and *A. trachycaulum*. Results of this analysis are in Table 4.4.

4.4.2.2 Plot C5:4

Stipa curtiseta was the only seeded species with no statistically significant difference in the number of plants between the high and low EC areas. However, the number of *S. curtiseta* plants were low in both areas with a total of four plants found in 30 quadrats. *A. subsecundum* and *Festuca hallii* were not found in the low EC area.

The remaining seeded species that were statistically significantly different between the high and low EC areas within C5:4 are *Agropyron smithii*, *A. trachycaulum* and *B. anomalus*. Results of this analysis are in Table 4.4.

4.4.2.3 Plot C4:8

A. subsecundum, B. anomalus, F. hallii and *Rumex occidentalis* do not have statistically significant differences in the number of plants between the high and low EC areas. However, three of these species did not have a representative in both the high and low EC areas and when present, had three or fewer plants: *A. subsecundum, F. hallii, R. occidentalis*. The seeded species that were statistically significantly different were *A. smithii*, *A. trachycaulum,* and *A. millefolium* and *P. procerus*. Results of this analysis are in Table 4.4.

4.4.3 Density of Seeded Species in High and Low EC Areas Among Plots

4.4.3.1 Density of Plant Species in Low EC Areas Among Plots

A. subsecundum and *F. hallii* did have statistically significant density differences, but in both plots each species were sparsely represented with three or fewer members. *A. smithii, A. trachycaulum* and *B. anomalus* had higher plant densities that were statistically significantly different, indicating that no consistent patterns were present. *Achillea millefolium* was seeded in two of the treatments, but observed in all low EC plots. The counts from three plots were analysed to determine that the density differences were statistically significant. *Penstemon procerus* was not included within this analysis since it was seeded in only one of the plots and was not observed in any plot. *Stipa curtiseta* was observed in only one plot and therefore was not included in this analysis. Results of this analysis are in Table 4.5.

The bar graphs, Figures 4.7, 4.8 and 4.9 illustrate that the density differences within the plots are observable and consistent relationships exist for most species within Plots C5:6 and C5:4. However, these relationships are not maintained in C4:8.

4.4.3.2 Density of Plant Species in High EC Areas Among Plots

Stipa curtiseta and *Festuca hallii* were the only species in this analysis that did not have statistically significant density differences. *S. curtiseta* was observed in two

of the three plots and had counts of three in each of the plots where it was observed, while *F. hallii* was also found in two of the three plots but had counts of three and five where it was observed. The low plant counts of *S. curtiseta* and *F. hallii* can be deemed statistically to be plants occurring by chance which diminishes the relevance of these results (Yeh 1997). *A. smithii, A. trachycaulum*, and *B. anomalus* had higher plant counts and statistically significant density differences, indicating that no consistent patterns are present. *Achillea millefolium* was seeded in two of the treatments, but was present in all three high EC plots, so the three counts were analysed and the resulting density differences were statistically significant. *Penstemon procerus* was also seeded in one treatment but counted in two high EC plots, the counts of which were used to determine that the density difference is statistically significant. *A. subsecundum* was not found more than once within any plot, so it was not analysed. Results of this analysis are in Table 4.5.

4.4.4 Competitive Influence of *Cirsium arvense*

The presence of *Cirsium arvense* within the quadrats in the low EC areas may have competitively excluded some seeded species. This species is found predominately in the low EC areas at the research site and when present in high EC areas it had a much smaller stature. However, the ranking analysis conducted on the plant counts of the seeded species and *C. arvense* within the permanent quadrats in the high and low EC areas did not result in a statistically significant difference in the density of the seeded species when *C. arvense* was present. The correlation coefficients also do not indicate that the presence of *C. arvense* caused a decline in the density of the seeded species. Therefore, the density of the seeded species in the plots is not negatively impacted by the presence of *C. arvense*. The density of *C. arvense* is in Table 4.6 and the results of the ranking analysis are in Table 4.7.

4.4.5 Research Results and Previous Research

Species diversity did not decline with increasing soil salinity at this research site. McGinnies et al. (1976), Bowman et al. (1985) and Kreeb et al. (1995) found evidence of vegetation patterns that coincided with soil salinity, but the concentrations of saline salts and sodium were higher at their respective research sites than at the

PARI Farm, where the degree of salinity may not have been high enough to cause a decline in species diversity.

The heterogeneous soil patches did not limit specific plant species to particular areas at this research site. McGinnies et al. (1976), Bowman et al. (1985) and Kreeb et al. (1995) found plant species distribution was limited by soil parameters. However, the higher concentrations of salts at their respective research sites may have produced more ranges of salinity from extremely saline to non-saline and therefore, created a greater variety of suitable microsites, producing more patchiness. In comparison, at this research site (at the PARI Farm), the generally lower concentrations of soil salinity may have produced less variability in soil salinity, so plant communities were more homogeneous.

The density of the seeded species was not consistent throughout the high EC or low EC areas at the research site and the density of the plant species was not lower in the high EC areas in two of the three plots. In comparison, McGinnies et al. (1976), Bowman et al. (1985) and Kreeb et al. (1995) observed lower plant densities in areas of higher SAR and EC, but conducted their respective research projects in areas with higher concentrations of SAR and EC than at the PARI Farm.

Species composition within the permanent quadrats does not denote the soils' EC conditions at this research site. The grass and forb species seeded at this site may have a higher tolerance for soil salinity, at least to the concentrations found at the research site and therefore, may be able to inhabit a variety of microsites. This could be similar to the *Plantago* species ability to inhabit sites with a variety of microsite conditions (Van Der Aart 1985).

4.5 Conclusion

Native plant species composition and/or density was not affected by soil salinity. Plant species found in greater densities in the high EC areas compared to the low EC areas in two of the three plots were under-represented in the remaining plot. No consistent pattern of increased density or diversity with low or high EC was apparent for any seeded plant species at the research site. The competitive effects of *C. arvense* did not significantly affect the density of the seeded species.

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Table 4.1 Density of Seeded Species Within Fifteen 0.1 m² Quadrats (1.5 m² total) at Plot C5:6 at the Research Site in 1997

	Low EC		High EC	
Species	**Total**	**Mean**	**Total**	**Mean**
Agropyron smithii	3	0.20	34	2.27
Agropyron subsecundum	0	0.00	0	0.00
Agropyron trachycaulum	22	1.47	56	3.73
Bromus anomalus	5	0.33	8	0.53
Festuca hallii	0	0.00	3	0.20
Stipa curtiseta	0	0.00	3	0.20

Table 4.2 Density of Seeded Species Within Fifteen 0.1 m² Quadrats (1.5 m² total) at Plot C5:4 at the Research Site in 1997

	Low EC		High EC	
Species	**Total**	**Mean**	**Total**	**Mean**
Agropyron smithii	1	0.07	19	1.27
Agropyron subsecundum	0	0.00	7	0.47
Agropyron trachycaulum	17	1.13	41	2.73
Bromus anomalus	14	0.93	40	2.67
Festuca hallii	0	0.00	5	0.33
Stipa curtiseta	1	0.07	3	0.20
Achillea millefolium	19	1.27	85	5.67
Monarda fistulosa	0	0.00	0	0.00
Oenothera biennis	0	0.00	0	0.00
Oxytropis deflexa	0	0.00	0	0.00
Oxytropis splendens	0	0.00	0	0.00

Table 4.3 Density of Seeded Species Within Fifteen 0.1 m² Quadrats (1.5 m² total) at Plot C4:8 at the Research Site in 1997

	Low EC		High EC	
Species	**Total**	**Mean**	**Total**	**Mean**
Agropyron smithii	38	2.53	11	0.73
Agropyron subsecundum	1	0.07	0	0.00
Agropyron trachycaulum	60	4.00	11	0.73
Bromus anomalus	48	3.20	61	4.07
Festuca hallii	3	0.20	0	0.00
Stipa curtiseta	0	0.00	0	0.00
Achillea millefolium	6	0.40	25	1.67
Monarda fistulosa	0	0.00	0	0.00
Penstemon procerus	0	0.00	8	0.53
Rumex occidentalis	2	0.13	0	0.00
Oenothera biennis	0	0.00	0	0.00

Table 4.4 Chi Square Analysis of the Density of Seeded Species Between High and Low EC Areas Within a Plot at the Research Site in 1997

Species	C5:6	C5:4	C4:8
		p-value	
Agropyron smithii	0.00	0.00	0.00
Agropyron subsecundum	NA	0.01	0.32
Agropyron trachycaulum	0.00	0.00	0.00
Bromus anomalus	0.41	0.00	0.21
Festuca hallii	0.08	0.03	0.08
Stipa curtiseta	0.08	0.32	NA
Achillea millefolium		0.00	
Monarda fistulosa		NA	
Oenothera biennis		NA	
Oxytropis deflexa		NA	
Oxytropis splendens		NA	
Achillea millefolium			0.00
Monarda fistulosa			NA
Penstemon procerus			0.00
Rumex occidentalis			0.16
Oenothera biennis			NA

NA: No plants were present in the low and high EC areas.
A p-value of 0.05 or less is required to reject the null hypothesis.

Table 4.5 Chi Square Analysis of the Density of Seeded Species in High and Low EC Areas Among All Plots at the Research Site in 1997

Species	High EC	Low EC
	p-value	
Agropyron smithii (3)	0.00	0.00
Agropyron subsecundum (3)	0.00	0.41
Agropyron trachycaulum (3)	0.00	0.00
Bromus anomalus (3)	0.00	0.00
Festuca hallii (3)	0.09	0.16
Stipa curtiseta (3)	0.22	NA
Achillea millefolium (2)	0.00	0.00
Monarda fistulosa (2)	NA	NA
Oenothera biennis (2)	NA	NA
Oxytropis deflexa (1)	NA	NA
Oxytropis splendens (1)	NA	NA
Penstemon procerus (1)	NA	NA
Rumex occidentalis (1)	NA	NA

NA: No plants were present in the low and high EC areas. The number in brackets after the species name represents the number of plots the species was seeded in.

A p-value of 0.05 or less is required to reject the null hypothesis.

Table 4.6 Density of *Cirsium arvense* Within Fifteen 0.1 m² Quadrats (1.5 m² total) at Each of the Three Plots at the Research Site in 1997

	Total	Mean
C5:6		
Low EC	41	2.73
High EC	1	0.07
C5:4		
Low EC	13	0.87
High EC	10	0.67
C4:8		
Low EC	16	1.07
High EC	1	0.07

Table 4.7 Ranking Analysis of the Density of *Cirsium arvense* versus the Seeded Species Within the Three Plots at the Research Site in 1997

	p-value
C5:6	
Low EC	0.64
High EC	0.10
C5:4	
Low EC	0.94
High EC	0.97
C4:8	
Low EC	0.53
High EC	0.26

A p-value of 0.05 or less is required to reject the null hypothesis.

Figure 4.1 Soil Surface EC Derived From Horizontal EM38 Readings at Plot C5:6 at the Research Site June 1997

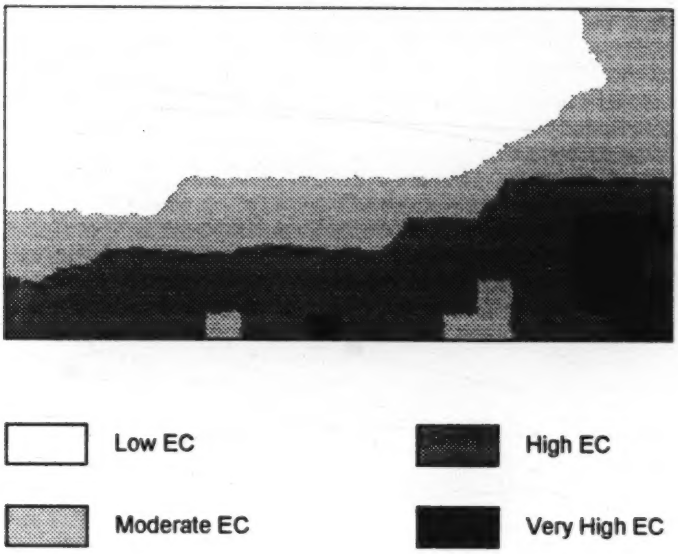
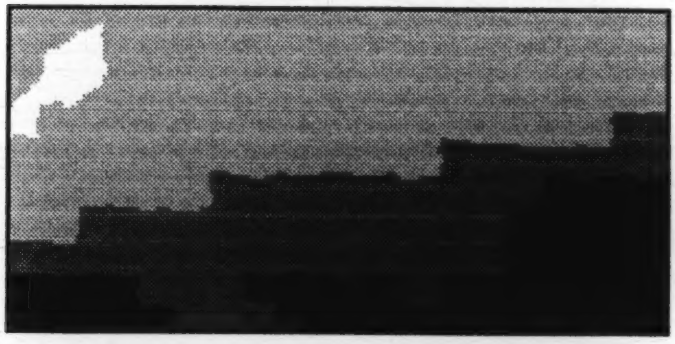


Figure 4.2 Subsoil EC Derived From Vertical EM38 Readings at Plot C5:6 at the Research Site June 1997



Low EC

Moderate EC

High EC

Very High EC

Figure 4.3 Soil Surface EC Derived From Horizontal EM38 Readings at Plot C5:4 at the Research Site June 1997

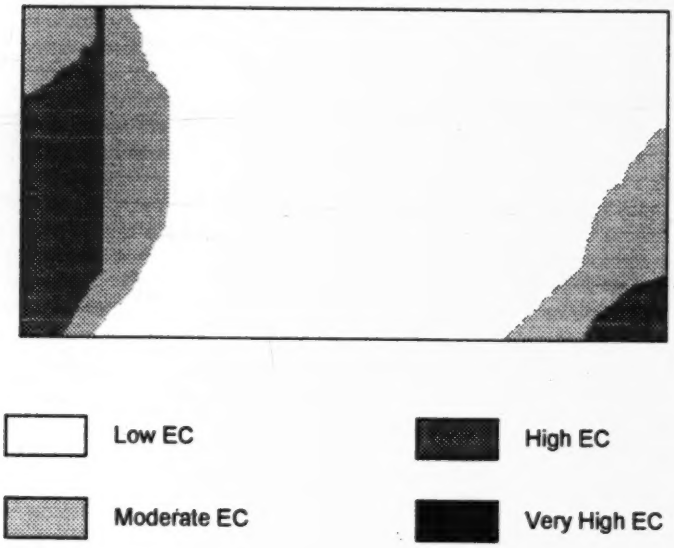
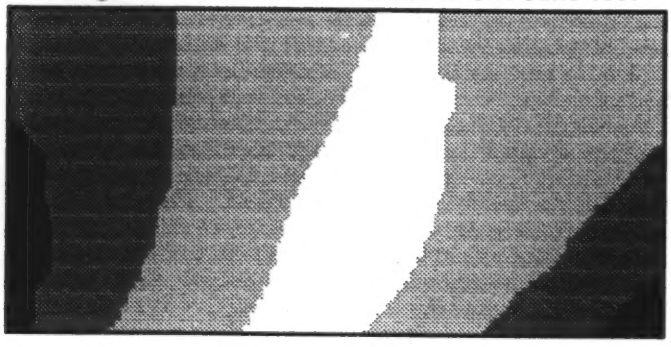


Figure 4.4 Subsoil EC Derived From Vertical EM38 Readings at Plot C5:4 at the Research Site June 1997



Low EC

High EC

Moderate EC

Very High EC

Figure 4.5 Soil Surface EC Derived From Horizontal EM38 Readings at Plot C4:8 at the Research Site June 1997

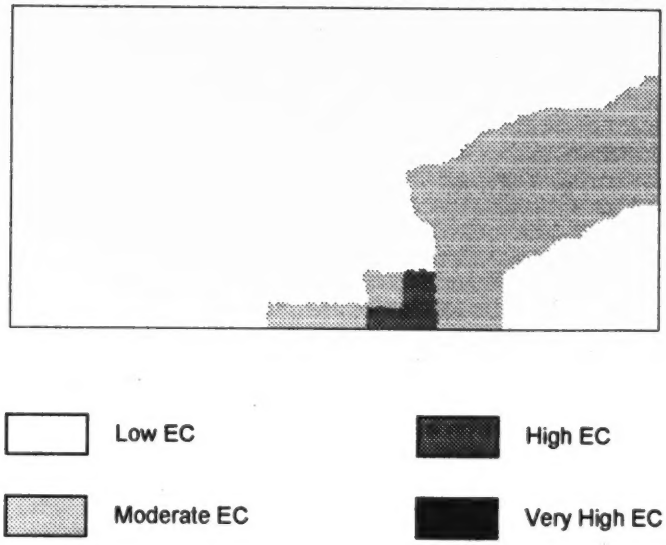


Figure 4.6 Subsoil EC Derived From Vertical EM38 Readings at Plot C4:8 at the Research Site June 1997

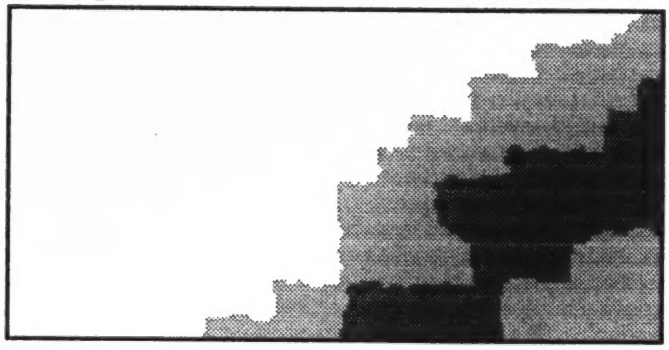


Figure 4.7 Plot C5:6 Seeded Plant Density Within Fifteen 0.1 m^2 Quadrats (1.5 m^2 Total) at the Research Site in 1997

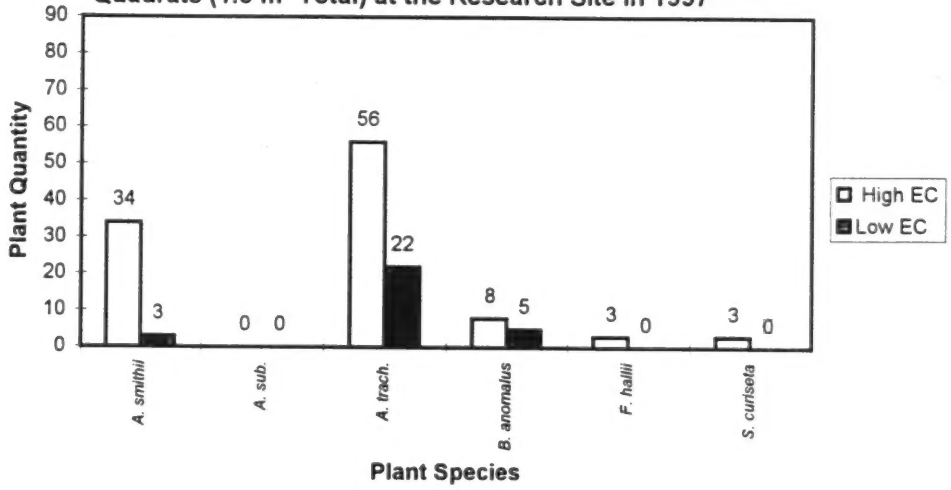


Figure 4.8 Plot C5:4 Seeded Plant Density Within Fifteen 0.1 m^2 Quadrats (1.5 m^2 Total) at the Research Site in 1997

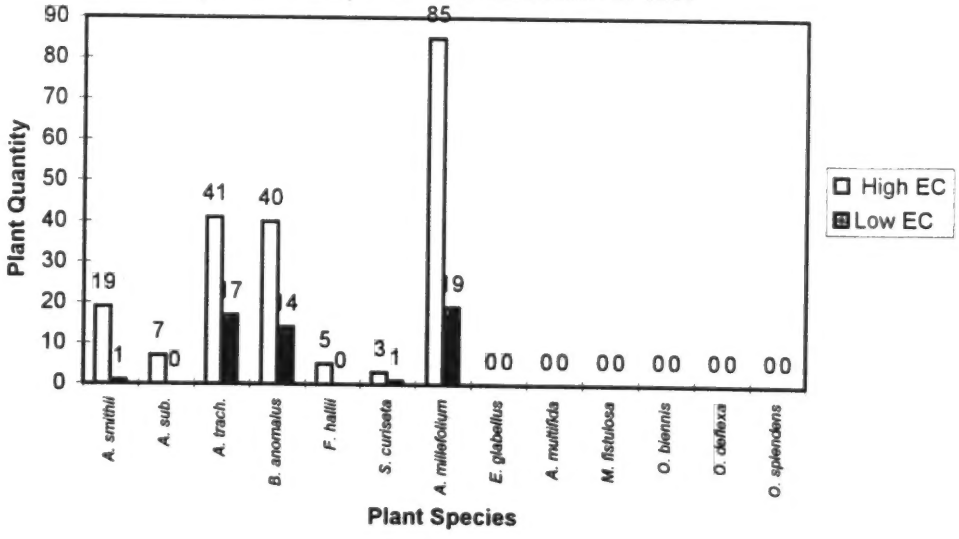
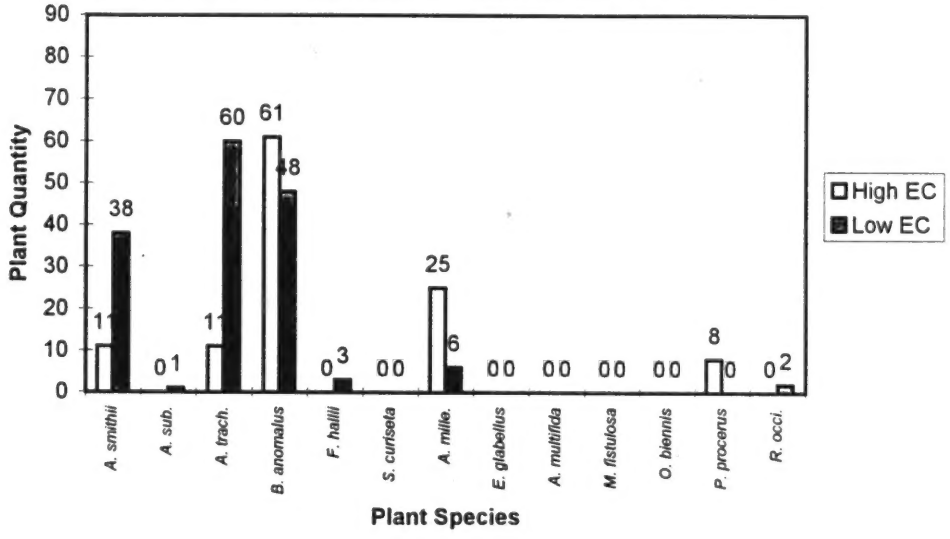


Figure 4.9 Plot C4:8 Seeded Plant Density Within Fifteen 0.1 m^2 Quadrats (1.5 m^2 Total) at the Research Site in 1997



CHAPTER 5
SYNTHESIS

5.1 Summary of the Research Conducted Within This Thesis

Plant community assembly processes cannot be predicted at the PARI Conservation Farm research site during the third and fourth growing seasons. Plant species do not seem to form plant communities that reflect the seed mix during these periods and perhaps since many seeded forbs are absent, the plant community will never be an exact representation of the seed mix. Some species of grasses are consistently dominant within each treatment and throughout the research site and are gaining further dominance within several treatments. Other species are maintaining their densities during the two growing seasons.

An association between soil salinity and plant species density is not apparent at the PARI Conservation Farm. Seeded grasses and forbs are not found in statistically significantly different quantities between the high and low EC areas. Therefore, plant community assembly processes on soils of differing EC conditions cannot be predicted.

5.2 Practical Applications of the Research Results

In practical terms, this research indicates that the plant community that develops from a specific seed mix cannot be predicted accurately. While some grasses are represented in proportion to the number of seeds in the seed mix, other forbs are under represented in the plant community compared to the seed mix. Perhaps the additional money spent on forbs within the seed mix was not worthwhile since most of these species are not currently represented in the plant community and are not likely to appear in the future. Instead, choosing one or two aggressive grass species such as *Agropyron trachycaulum*, *A. smithii* and *Bromus anomalus* may provide good ground cover within a reasonably short time period. For wellsites where brine spills have occurred, some of the seeded species used in this research will be able to tolerate moderate salinity such as *Agropyron trachycaulum*, *A. smithii, Bromus anomalus* and *Achillea millefolium* as well as provide cover on non-saline soils.

5.3 Research Results compared to Previous Research

In relation to the research that has been conducted on plant growth on salt-affected soils, this research indicates that in the third and fourth growing seasons, many species are not confined to non-saline soils and vegetation patterns that denote the saline soil areas are not evident. McGinnies et al. (1976), Bowman et al. (1985) and Kreeb et al. (1995) found that plant species diversity declines on saline soils above a threshold value and plant species density also declines on saline soils, but the concentration of salts and sodium at their respective research sites were generally much higher than at this research site.

The theories proposed for how plant community assembly processes form unique plant communities cannot be verified or rejected by this research. Species diversity is statistically consistent across all treatments although the heterogeneity of the soils is apparent from the soil surveys done on the research site (Walker 1992). This information tends to contradict Levin's (1974) research which contends that species richness should increase with the heterogeneity of the landscape. Species density is becoming more variable for many grass species, but the majority of the forbs are rare or absent. The total number of seeded plants within the treatments is more variable in the fourth growing season compared to the third and the densities of some grass species is increasing in greater proportion compared to the total number of seeded plants.

With so many variables to consider, it is difficult to discern which processes are governing plant community assembly. Since all treatments have the same short history it is difficult to use Drake's (1991) theory as an explanation. Initial conditions, including nutrient availability, were probably quite variable, which Wilson (1992) and Tilman (1982) would subscribe to being important determinants of the community assembly outcome. Pickett et al. (1987) and Diamond's (1975) research focuses more on disturbances within a plant community and the resulting competition provided by the species that were undisturbed, which is not applicable to this research site since the entire site was cultivated prior to seeding. Competition is occurring from the species present in the natural seed bank, but the plant community is essentially starting with an equal opportunity for all seeds to develop into a plant community.

5.4 Field Studies versus Greenhouse Research

The variability in field studies provides a unique opportunity to determine if plant assembly processes are occurring. The changes observed in the density of each plant species and the diversity within each treatment cannot be duplicated in a greenhouse. Certainly a plant species could be seeded in a greenhouse and observed to determine its germination rate and consequential survival over a simulated winter, but the direct assumption that this species would therefore produce the same results in the field would be erroneous. Plant species may develop into plant communities based on microsite conditions or other, yet to be determined, factors or processes. As well, a greenhouse study would not provide an opportunity to study the heterogeneous nature of the soils of the research site as they affect plant growth and plant community development.

Conversely, obtaining plant density data in the field has ample room for incorrect interpretation. In this study, if one plant species would have been confined to low EC areas only, would that infer that this plant species will not grow in high EC areas at any reclamation site or be found in high EC areas in an undisturbed area? Other variables may have confined that species to low EC areas: soil nutrients, soil texture, competition from other plant species, pests, grazing by deer or other animals, and/or weather conditions over the past two years. Therefore, a definitive statement about a species' ability to tolerate specific conditions could not be made as an all-encompassing statement or used to disregard an earlier theory.

Plant community development is even more susceptible to acceptance of incorrect rules. Without long term studies in a variety of microsites throughout an ecosystem and other similar ecosystems, it is impossible to suggest what factors are the main factors in plant community development, if any, and whether the development of a plant community can be predicted at all.

5.5 Future Research

Long term studies are needed to determine the ability of specific plant species to form plant communities on saline and non-saline soils. For future research projects, more control of soil salinity would be recommended, even if adding salts to the research site was required to achieve salinity levels equal to brine spills. Furthermore, exact numbers of seeds within an area with a tested germination rate would provide a

better representation of germination and consequently survivability in saline soils. A seed bank analysis could provide information on whether seeds of those species were already present in the soil and may skew the seeded plant density data. Several replicates of each treatment would be necessary and control sites on non-saline soils using the same species in the same density is also essential. A complete analysis of the soil nutrient status should also be conducted for all treatment sites in sufficient detail to provide information as to whether a confounding variable could be altering the plant density results.

Plant community assembly processes require a long term study in a heterogeneous environment that is preferably free of aggressive, noxious weeds that shorten the life span of the research site, unless selective intervention is taken. Although aggressive, noxious weeds are often part of many reclamation sites, control through broadleaf herbicides is often undertaken to ensure the issuance of a reclamation certificate. In a research site, this type of intervention may contravene and influence plant community development processes, relegating the acceptance or rejection of a hypothesis to a questionable status.

Even without the presence of non-seeded species, the large number of environmental variables will make determination of specific assembly processes difficult to determine accurately, no matter how many soil analyses are conducted in conjunction with monitoring other measurable factors. This type of research is difficult to conduct in the field, but would be meaningless in a greenhouse environment.

Until more information based on sound research practices is available, it may suffice to know with some confidence that a seed mix designed for reclamation will produce a native plant community which provides good ground cover and is not a monoculture. This seed mix could be composed of *Agropyron, Achillea* and *Bromus* species for example. Whether it is important to have precise knowledge that there will be a certain proportion of a specific plant species will depend on the reclamation site and the goals of the reclamation project. If the goal is to revegetate the area with native species which will provide a good protective cover against soil erosion, then planting twelve species may be over-indulgent when four species would satisfy the goal. Conversely, if the area is designated as public lands, the choice of ten or more species could be justified as part of a restoration attempt. However, even if it were possible to know with certainty what the plant community would resemble after a few

growing seasons, it will still be impossible to predict the long term density and diversity of the plant community, given nature's sometimes chaotic personality.

5.6 Literature Cited

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APPENDIX A

Figure A.1 Research Site Map (1996 and 1997)

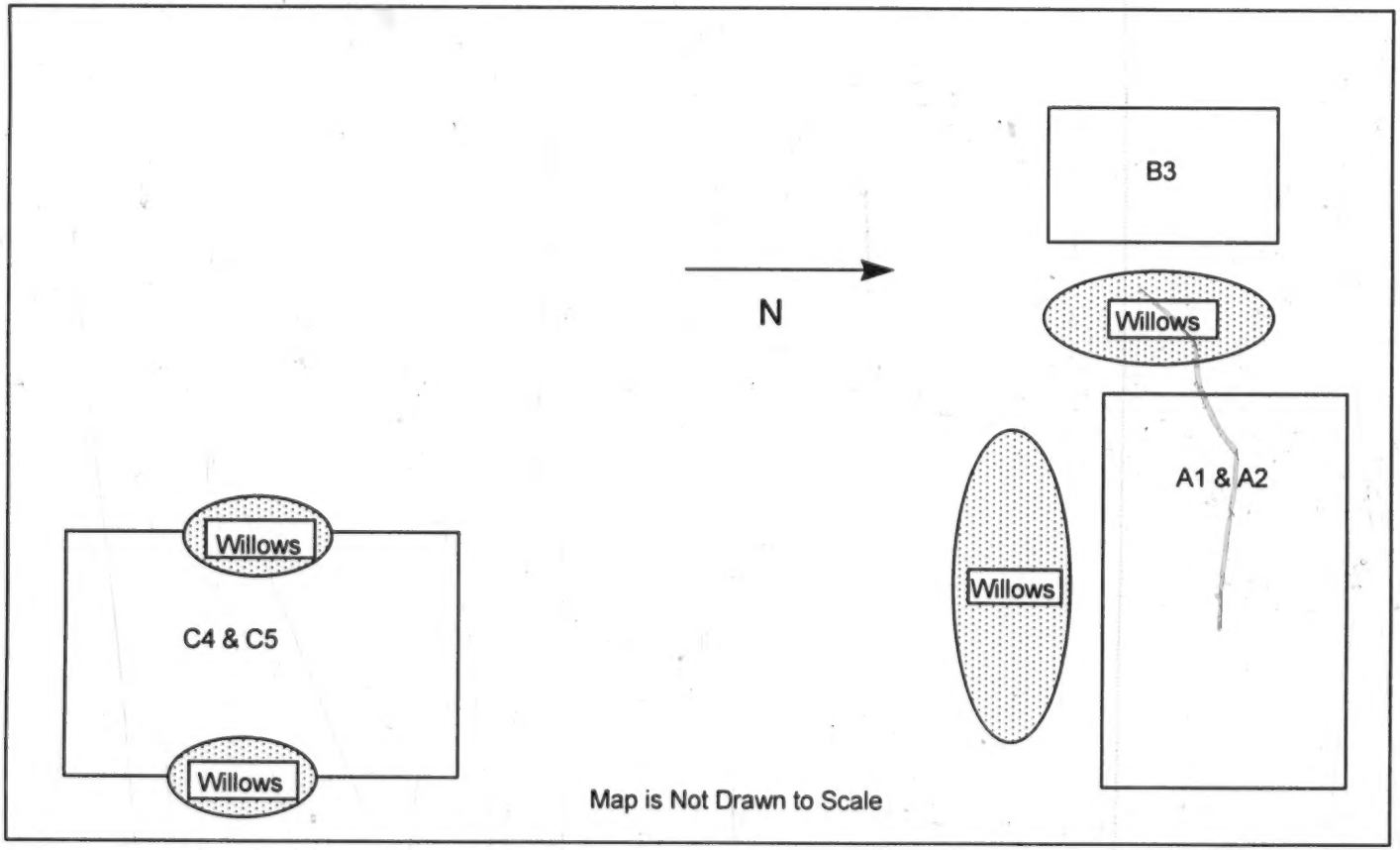


Figure A.2 Blocks A1, A2 and B3 at the Research Site in 1996 and 1997

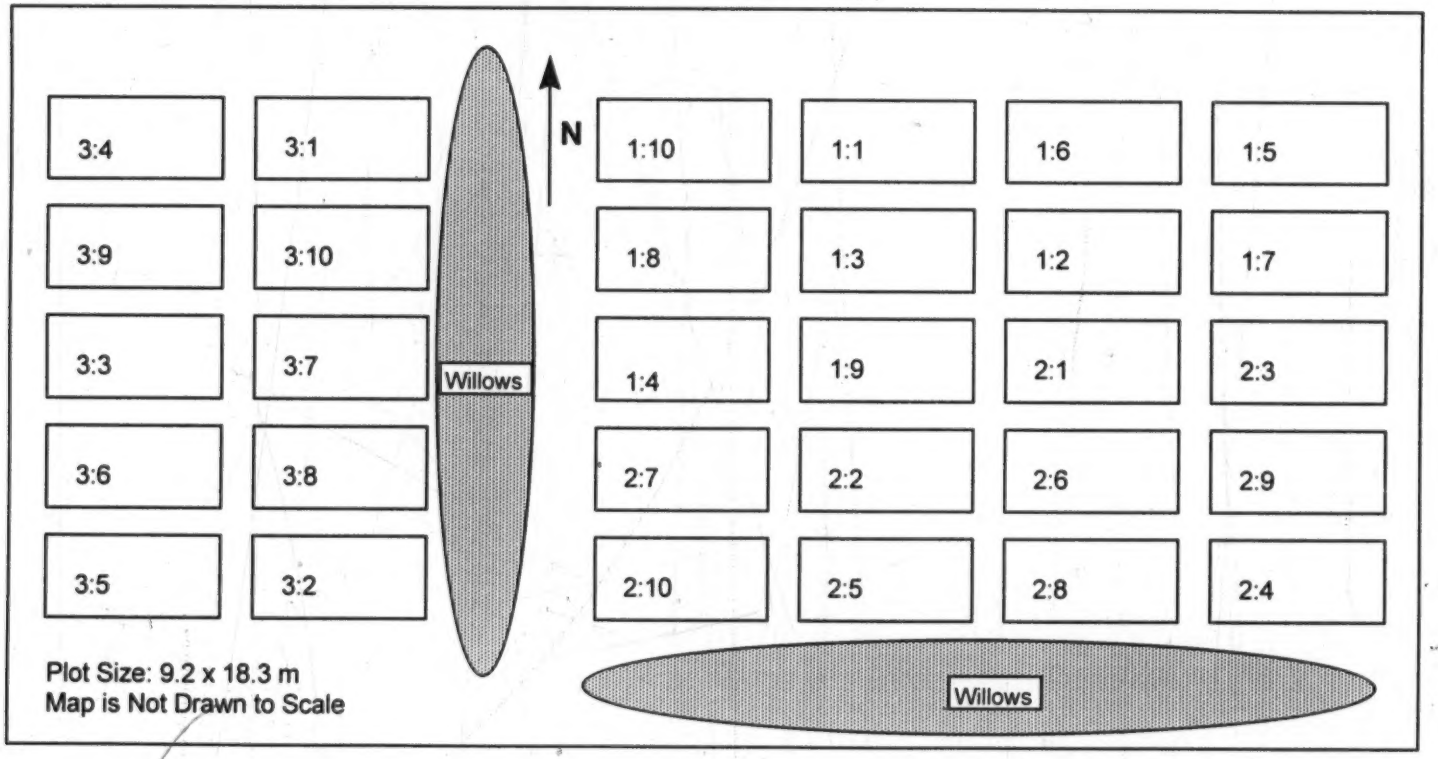
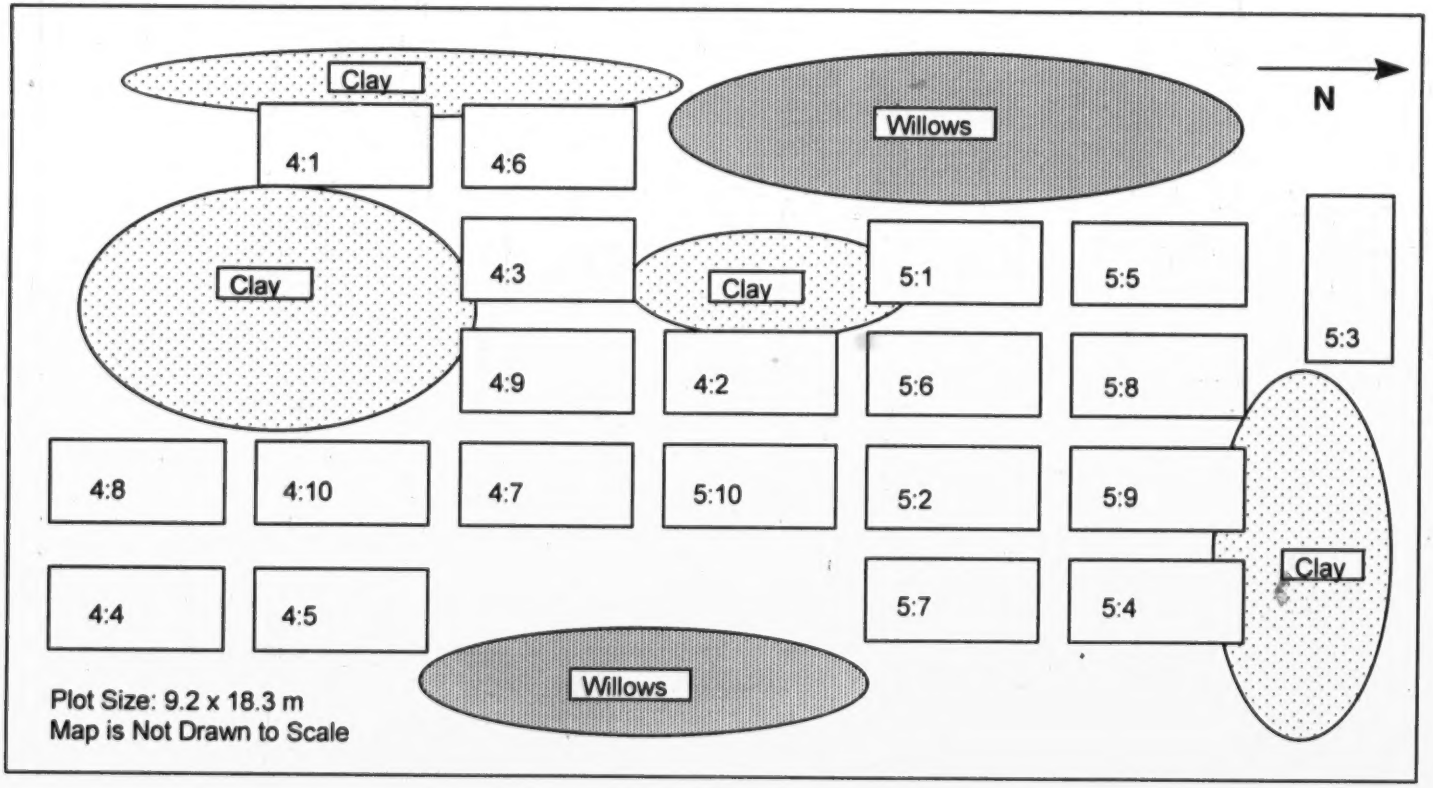


Figure A.3 Blocks C4 and C5 at the Research Site in 1996 and 1997



APPENDIX B

Table B.1 Seeded Species and Seeding Rate in Pure, Live Seeds (PLS) per m^2 at the Research Site in 1994

		PLS m^{-2}
Seed Mix: 1		
Agropyron smithii Rydb.	Western wheatgrass	37
Agropyron subsecundum (Link) Hitchc.*	Awned wheatgrass	27
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	22
Bromus anomalus Rupr. *ex* Fourn.	Nodding brome	134
Festuca hallii (Vasey) Piper**	Plains rough fescue	111
Stipa curtiseta (A. S. Hitchc.) Barkworth	Western porcupine grass	65
Seed Mix: 2		
Agropyron smithii Rydb.	Western wheatgrass	27
Agropyron subsecundum (Link) Hitchc.*	Awned wheatgrass	37
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	29
Bromus anomalus Rupr. *ex* Fourn.	Nodding brome	97
Festuca hallii (Vasey) Piper**	Plains rough fescue	81
Stipa curtiseta (A. S. Hitchc.) Barkworth	Western porcupine grass	47
Bouteloua gracilis (HBK) Lag.(B)	Blue grama grass	5
Bromus ciliatus L.	Fringed brome	11
Koeleria macrantha (Ledeb.) J. A. Schultes (B)	June grass	60
Poa palustris L. (B)	Fowl bluegrass	86
Stipa comata Trin. & Rupr.	Spear grass	18
Stipa viridula Trin.	Green needle grass	36
Seed Mix: 3		
Agropyron smithii Rydb.	Western wheatgrass	27
Agropyron subsecundum (Link) Hitchc.*	Awned wheatgrass	19
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	16
Bromus anomalus Rupr. *ex* Fourn.	Nodding brome	97
Festuca hallii (Vasey) Piper**	Plains rough fescue	81
Stipa curtiseta (A. S. Hitchc.) Barkworth	Western porcupine grass	47
Achillea millefolium L. (B)	Common yarrow	6
Anemone multifida Poir.	Cut-leaved anemone	6
Erigeron glabellus Nutt. (B)	Fleabane	14
Monarda fistulosa L. (B)	Bergamot	14
Oenothera biennis L. (B)	Yellow evening primrose	7
Penstemon procerus Dougl. *ex* Grah. (B)	Slender blue beard-tongue	7
Rumex occidentalis S. Wats	Western dock	7

Table B.1 Seeded Species and Seeding Rate in Pure, Live Seeds (PLS) per m^2 at the Research Site in 1994 (con't)

		PLS m^{-2}
Seed Mix: 4		
Agropyron smithii Rydb.	Western wheatgrass	27
Agropyron subsecundum (Link) Hitchc.*	Awned wheatgrass	19
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	16
Bromus anomalus Rupr. *ex* Fourn.	Nodding brome	97
Festuca hallii (Vasey) Piper**	Plains rough fescue	81
Stipa curtiseta (A. S. Hitchc.) Barkworth	Western porcupine grass	47
Achillea millefolium L. (B)	Common yarrow	6
Anemone multifida Poir.	Cut-leaved anemone	6
Erigeron glabellus Nutt. (B)	Fleabane	14
Monarda fistulosa L. (B)	Bergamot	14
Oenothera biennis L. (B)	Yellow evening primrose	3
Oxytropis splendens Dougl. *ex* Hook. *(B)*	Showy locoweed	14
Oxytropis deflexa (Pall.) DC. (B)	Reflexed locoweed	39
Seed Mix: 5		
Agropyron riparian Rydb.	Streambank wheatgrass	108
Agropyron smithii Rydb.	Western wheatgrass	55
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	80
Festuca hallii (Vasey) Piper**	Foothills rough fescue	163
Festuca ovina L.	Sheep's fescue	121
Festuca rubra L.	Creeping red fescue	74
Koeleria macrantha (Ledeb.) J. A. Schultes (B)	June grass	60
Poa alpina L.	Alpine bluegrass	60
Stipa viridula Trin.	Green needle grass	33
Seed Mix: 6		
Agropyron smithii Rydb.	Western wheatgrass	27
Agropyron subsecundum (Link) Hitchc.*	Awned wheatgrass	19
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	16
Bromus anomalus Rupr. *ex* Fourn.	Nodding brome	169
Festuca hallii (Vasey) Piper**	Plains rough fescue	172
Stipa curtiseta (A. S. Hitchc.) Barkworth	Western porcupine grass	47
Seed Mix: 7		
Agropyron smithii Rydb.	Western wheatgrass	17
Agropyron subsecundum (Link) Hitchc.*	Awned wheatgrass	29
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	23
Bromus anomalus Rupr. *ex* Fourn.	Nodding brome	134
Festuca hallii (Vasey) Piper**	Plains rough fescue	142
Stipa curtiseta (A. S. Hitchc.) Barkworth	Western porcupine grass	30
Bouteloua gracilis (HBK) Lag. (B)	Blue grama grass	2
Bromus ciliatus L.	Fringed brome	6
Koeleria macrantha (Ledeb.) J. A. Schultes (B)	June grass	89
Poa palustris L. (B)	Fowl bluegrass	125
Stipa comata Trin. & Rupr.	Spear grass	9
Stipa viridula Trin.	Green needle grass	55

Table B.1 Seeded Species and Seeding Rate in Pure, Live Seeds (PLS) per m^2 at the Research Site in 1994 (con't)

		PLS m^{-2}
Seed Mix: 8		
Agropyron smithii Rydb.	Western wheatgrass	17
Agropyron subsecundum (Link) Hitchc.*	Awned wheatgrass	12
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	10
Bromus anomalus Rupr. *ex* Fourn.	Nodding brome	134
Festuca hallii (Vasey) Piper**	Plains rough fescue	142
Stipa curtiseta (A. S. Hitchc.) Barkworth	Western porcupine grass	30
Achillea millefolium L. (B)	Common yarrow	4
Anemone multifida Poir.	Cut-leaved anemone	9
Erigeron glabellus Nutt. (B)	Fleabane	22
Monarda fistulosa L. (B)	Bergamot	9
Oenothera biennis L. (B)	Yellow evening primrose	3
Penstemon procerus Dougl. ex Grah. (B)	Slender blue beard-tongue	11
Rumex occidentalis S. Wats.	Western dock	5
Seed Mix: 9		
Agropyron smithii Rydb.	Western wheatgrass	17
Agropyron subsecundum (Link) Hitchc.*	Awned wheatgrass	12
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	10
Bromus anomalus Rupr. *ex* Fourn.	Nodding brome	134
Festuca hallii (Vasey) Piper**	Plains rough fescue	142
Stipa curtiseta (A. S. Hitchc.) Barkworth	Western porcupine grass	30
Achillea millefolium L. (B)	Common yarrow	4
Anemone multifida Poir.	Cut-leaved anemone	10
Erigeron glabellus Nutt. (B)	Fleabane	22
Monarda fistulosa L. (B)	Bergamot	9
Oenothera biennis L. (B)	Yellow evening primrose	3
Oxytropis splendens Dougl. *ex* Hook.*(B)*	Showy locoweed	20
Oxytropis deflexa (Pall.) DC. (B)	Reflexed locoweed	19
Seed Mix: 10		
Agropyron dasystachyum (Hook.) Scribn.	Northern wheatgrass	71
Agropyron intermedium (Host) Beauv.***	Intermediate wheatgrass	16
Agropyron smithii Rydb.	Western wheatgrass	53
Agropyron subsecundum (Link) Hitchc.*	Awned wheatgrass	9
Agropyron trachycaulum (Link) Malte	Slender wheatgrass	12
Medicago sativa L.	Alfalfa	8
Stipa viridula Trin.	Green needle grass	104

Authorities from Moss (1992) unless otherwise noted.
* Authority from Hardy BBT (1989).
** Authority from Pavlisk and Looman (1984).
B = Broadcast seeded.
Species without a (B) were drill seeded.

Table B.2 Latin and Common Names of Unseeded Species at the Research Site During 1996 and 1997

Latin Name	Common Name
Agrostis scabra Willd.	Rough hair grass or tickle grass
Amelanchier alnifolia Nutt.	Saskatoon
Artemisia absynthium L.	Wormwood
Artemisia frigida Willd.	Pasture sage
Axyris amaranthoides L.	Russian pigweed
Bromus inermis Leyss.	Smooth brome grass
Carex spp. L.	Sedge
Cirsium arvense (L.) Scop.	Canada thistle
Crepis tectorum L.	Annual hawksbeard
Delphinium glaucum S. Wats.	Larkspur
Elaeagnus commutata Bernh. *ex* Rydb.	Silverberry
Epilobium angustifolium L.	Fireweed
Fragaria virginiana Duchesne	Wild strawberry
Galium boreale L.	Northern bedstraw
Geum spp. L.	Avens
Oryzopsis asperifolia Michx.	Rough-leaved rice grass
Plantago major L.	Common plantain
Plantago spp. L.	Plantain
Poa pratensis L.	Kentucky bluegrass
Polygonum convolvulus L.	Wild buckwheat
Potentilla norvegica L.	Rough cinquefoil
Rosa acicularis Lindl.	Wild rose
Schizachne purpurascens (Torr.) Swallen	Purple oat grass
Sonchus spp. L.	Sow thistle
Symphoricarpos albus (L.) Blake	Snowberry
Symphoricarpos occidentalis Hook.	Buckbrush
Taraxacum officinale Weber	Common dandelion
Thalictrum venulosum Trel.	Vieny meadow rue
Thlaspi arvense L.	Stinkweed

Authorities from Moss (1992).

Table B.3 Soils at the Research Site, 1992 and 1993 Soil Surveys

Blocks A:1 and A:2 Hobbema-Beaver Hills

Parent Material and Landform:
Discontinuous, moderately fine to medium textured, fluviolacustrine or glaciolacustrine (FLLC or GLLC) veneer overlying moderately fine textured till.
Slopes: 2-9%.

Major Soils:
HBMzz (O.BL) 20-40%
BVH (O.BL) 20-30%
JVExtaa/JVEaa (HU.LG) 20-30%
SZ Group (NRM, STExt, CMO, TFD) 15-20%

Minor Soils:
POK/POKzz (E.BL/O.BL) 5%

Remarks:
Undulating to hummocky moraine with a thin, discontinuous, FLLC or GLLC veneer. Commonly, till soils (BVH) occur on the hilltops and may have thin A horizons; veneer soils (HBMzz) occur on the side slopes; and wet soils (mainly HU.LG and some O.HG) occupy lower slopes and depressions. Solonetizic soils and like soils (NRM, STExt, CMO) occur randomly on mid-slope to hilltop positions, usually where salts (i.e. gypsum) are near the surface. Wet soils (mainly HU.LG) occupy depressions and channels.

Block B:3 Angus Ridge-Norma

Parent Material and Landform:
Moderately fine textured till. Undulating to hummocky.
Slopes 2-5%.

Major Soils:
AGSsc (E.BL) 20-30%
NRMsc (SZ.BL) 20-30%
JVExtaa/JVEaa (HU.LG) 20-30%
Gleyed saline/carbonated soils 10-20%

Minor Soils:
TFD/CMO (BL.SO/BL.SS) 5-15%
BVH (O.BL) 5%
HBM/STExt (E.BL/SZ.BL) 5%

Remarks:
Undulating moraine with only minor veneer. The major soils commonly have saline subsoil (sc modifier) and occur on mid slopes and hilltops. Gleyed Rego Blacks and related soils with carbonated and/or re-salinized mid to upper sola are common on lower slopes. Recharge gleysols (HU.GL) occupy most depressions.

Table B.3 Soils at the Research Site, 1992 and 1993 Soil Surveys (con't)

Blocks C:4 and C:5 Camrose-Norma

Parent Material and Landform:
Moderately textured till. Undulating and hummocky. Slopes 2-5%.

Major Soils:
CMOta (BL.SS) 30-40%
NRM (SZ.BL) 20-30%
JVExtaa/JVEaa (HU.GL) 15-25%

Minor Soils:
ARM/STExt (BL.SS/SZ.BL) 5-15%
TFD (BL.SO) 5-15%
BVH/AGS (O.BL/E.BL) 5%

Remarks:
Undulating to hummocky moraine. Commonly, Solonetzic Blacks (NRM) occur on the hilltops, Solodized Solonetz (CMO) occur on the mid to lower slopes and bench-like areas, and wet soils (mainly HU.LG) occupy depressional segments of the landscape. Solods (TFD) are common inclusions, occurring from hilltops to mid slopes. Veneer soils (FLLC or GLLC) over till are also common inclusions.

Description of the Soils at the Research Site:

Angus Ridge (AGS) Thick Black Eluviated Black Chernozem
Soils developed on clay loam textured till. Cultivation may incorporate the AE horizon into the AP horizon.

Armena (ARM) Black Solodized Solonetz
Loam soil developed on alluvial lacustrine material. Underlying till is within the solum and there is often a coarse-textured layer at the contact. Fairly well to well drained.

Beaverhills (BVH) Thick Black Orthic Black Chernozem
This soil is a clay loam textured till and is associated with a high water table in spring.

Camrose (CMO) Thick Black, Black Solodized Solonetz
These soils have a BNT horizon that is undesirable. The separation of the topsoil from the subsoil is difficult unless an AE horizon is present. The lower subsoil is saline and sodic. The water table is high in spring.

Hobbema (HBM) Thick Black Eluviated Black Chernozem
Soil developed on silty clay loam grading to silt loam texture veneers with clay loam till occurring about 30 to 70 cm below the surface. In cultivated areas, the AE horizon is usually incorporated into the plow layer (AP horizon). Soils usually associated with stream channels.

Table B.3 Soils at the Research Site, 1992 and 1993 Soil Surveys (con't)

Description of the Soils at the Research Site: (con't)

Jarvie (JVE) Dark Gray-Gray Humic Luvic Gleysol
These soils are wet year round, due to a seasonally high water table, resulting in unstable faces where exposed.

Norma (NRM) Thick Black Solonetzic Black Chernozem
Soils of this series have a B horizon with Solonetizic tendencies. The lower subsoil is saline and sodic.

Ponoka (POK) Eluviated Black Chernozem
This soil is formed from medium textured fluvial or lacustrine parent material and is associated with mesic areas.

Sante (STE) Solonetzic Black
This soil has the same parent geological material as the Ponoka series (fluvial or lacustrine material) and has a Solonetzic B horizon.

Tofield (TFD) Black Solod
Soils of this series are formed from moderately fine till and have temporary ponding.

Modifying codes associated with some series:
aa=not modal with the soil correlation area
sc= saline subsoil
ta=thin A horizon
xt=till at 30-99 cm
zz=Atypical subgroup

(Pedocan Land Evaluation 1993; Walker 1992)

B.1 Literature Cited

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